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A Workshop entitled "Algal Management and Control" was held 9-12 March 1980 at the Asilomar Conference Center, Pacific Grove, Calif., to review state-of-the-art techniques for the management and control of lacustrine algal populations, to establish the functional availability and limits of various algal management and control techniques, and to determine research needs in relation to the further development of algal management and control techniques. This report presents the Proceedings of the Workshop. A Bibliography of research on algicides and algal management is also presented in this report.

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PREFACE

These Proceedings resulted from a Workshop entitled "Algal Management and Control" held at the Asilomar Conference Center, Pacific Grove, California. The objectives of the Workshop were:

a. To review state-of-the-art techniques for the management and control of lacustrine algal populations.

b. To establish the functional availability and limits of various algal management and control techniques.

c. To determine research needs in relation to the further development of algal management and control techniques.

The Algal Management and Control Workshop was conducted by the U. S. Environmental Protection Agency's Environmental Monitoring Systems Laboratory, Las Vegas, Nevada, and was sponsored by the U. S. Army Corps of Engineers Waterways Experiment Station's (WES) Environmental and Water Quality Operational Studies (EWQOS) Program under Interagency Agreement No. EPA-IAG-78-R-X0383. EWQOS is sponsored by the Office, Chief of Engineers, U. S. Army.

The Workshop consisted of formal reviews of approaches or perspectives to be considered in the management and control of algal populations; plenary discussions; and formal panel deliberations. The participants also spent many hours of their time participating in informal discussions of algal management and control. These contributed greatly to the success of the Workshop.

The Workshop Proceedings were edited and compiled by William D. Taylor, University of Nevada, Las Vegas, and V. W. Lambou, U. S. Environmental Protection Agency. Stephen C. Hern, U. S. Environmental Protection Agency, Las Vegas, and Jeffrey J. Janik, Linda S. Blakey, and Marsha K. Morris, University of Nevada, Las Vegas, assisted Lambou and Taylor in making arrangements for the Workshop and summarizing the Proceedings. Workshop planning and coordination were provided by V. W. Lambou, W. D. Taylor, and John W. Barko of the WES. Dr. Jerome L. Mahloch was Project Manager for EWQOS, and Dr. John Harrison was Chief of the Environmental Laboratory, WES.

The Commander and Director of WES during the conduct of the Workshop was Col. Nelson P. Conover, CE. Technical Director of WES was Mr. Fred R. Brown.

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PARTICIPANTS AND CONTRIBUTORS

John Barko
U.S. Army Engineers Waterways
Experiment Station
Corps of Engineers
P.O. Box 631
Vicksburg, MS 39180

*Linda S. Blakey
Department of Biology
University of Nevada at Las Vegas
Las Vegas, NV 89154

*Jeffrey C. Burnham
Department of Microbiology
Medical College of Ohio
C.S. 10008
Toledo, OH 43699

*G. Dennis Cooke
Department of Biological Sciences
Kent State University
Kent, OH 44242

*Thomas Crisman
Department of Environmental Engineering
Sciences
University of Florida
Gainesville, FL 32611

*Paul R. Desjardins
Department of Plant Pathology
University of California
Riverside, CA 92521

Robert Engler
U.S. Army Engineers Waterways
Experiment Station
Corps of Engineers
P.O. Box 631
Vicksburg, MS 39180

Gerald J. Filbin
U.S. Army Engineers Waterways
Experiment Station
P.O. Box 631
Vicksburg, MS 39180

*George P. Fitzgerald
Algae Acres
3644 Rivercrest Road
McFarland, WI 53558

Douglas Gunnison
U.S. Army Engineers Waterways
Experiment Waterways
Corps of Engineers
P.O. Box 631
Vicksburg, MS 39180

*Stephen C. Hern
U.S. Environmental Protection Agency
Environmental Monitoring Systems
Laboratory
P.O. Box 15027
Las Vegas, NV 89114

*Jeffrey J. Janik
Department of Biology
University of Nevada at Las Vegas
Las Vegas, NV 89154

**Kathleen I. Keating
6 Webb Court
Park Ridge, NJ 07656

*Robert Kennedy
U.S. Army Engineers Waterways
Experiment Station
Corps of Engineers
P.O. Box 631
Vicksburg, MS 39180

Douglas Knauer
Wisconsin Department of Natural
Resources
Office of Inland Lake Renewal
P.O. Box 7921
Madison, WI 53701

*Victor W. Lambou
U.S. Environmental Protection Agency
Environmental Monitoring Systems
Laboratory
P.O. Box 15027
Las Vegas, NV 89114

---

* Contributors.
** Paper submitted in absentia.

David P. Larsen
U.S. Environmental Protection Agency
200 SW 35th Street
Corvallis, OR 97330

*Marc W. Lorenzen
Environmental Systems
Tetra Tech, Inc.
1900 116th Avenue, NE
Suite 200
Bellevue, WA 98004

*Marsha K. Morris
Department of Biology
University of Nevada at Las Vegas
Las Vegas, NV 89154

Joseph Norton
U.S. Army Engineers Waterways
Experiment Station
Corps of Engineers
P.O. Box 631
Vicksburg, MS 39180

W. J. Oswald
College of Engineering
Office of Research Services
Sanitary Engineering Res. Lab.
University of California
Berkeley, CA 94720

*Karen B. Porter
Department of Zoology
University of Georgia
Athens, GA 30601

*Gerald W. Prescott
11123 Starr Road
RFD 2
Wyoming, NY 14591

Joseph Shapiro
Limnological Research Center
University of Minnesota
220 Pillsbury Hall
310 Pillsbury Dr., SE
Minneapolis, MN 55455

*William D. Taylor
Department of Biology
University of Nevada at Las Vegas
Las Vegas, NV 89154

Cornelius I. Weber
Aquatic Biology Section
EMSL, Cincinnati
Environmental Protection Agency
Room 567
Cincinnati, OH 45268

*Eugene B. Welch
Department of Civil Engineering, FX-10
University of Washington
Seattle, WA 98195

Robert G. Wetzel
M.S.U. Kellogg Biological Station
3700 Gull Lake Drive
Hickory Corners, MI 49060

---

* Contributors.
** Paper submitted in absentia.

A REVIEW OF CONTROL MEASURES FOR OBJECTIONAL ALGAL "BLOOMS"

Gerald W. Prescott

Emeritus Professor of Botany
University of Montana
Missoula, Montana 59801

The history of algicides and algistatic control for lakes and reservoirs, as is true for the history of almost any evolution, is interlocked with or paralleled by others. For example, the development of algal control and especially of algicide applications has come to be what it is today partly through the slow, historical realization that water is a carrier of disease and that water quality merits concerned attention. Today it seems almost curious that illness and disease were scarcely associated with biological contamination over such a long period of time. That there was some notion that microorganisms might be responsible for or related to disease is illustrated by a belief that granules in desmids were the cause of swamp fever or malaria in Italy (Ref. Fischer 1884).

The history of algicides is related to the slowly evolving demand for better tastes and odor in drinking water, at the same time that it should be sterile. The changing and perhaps evolution of aesthetic notions concerning the appearance of lakes, and their use for recreation is collateral with algicide development. Objectionable eutrophication, proceeding logarithmically as it does, has led to the desirability to control algal blooms. Such blooms, especially of blue-green algae,came to be recognized as a reflection of and a contribution to eutrophication. Hence some of the facets of limnology have evolved with efforts to explain and to control superabundant growths of algae.

The recurrent and widespread deaths of fish, aquatic birds and of land animals using algal-infested waters have given impetus to the search for algicides and the development of algal control measures. In many ways, the history of the industrial age, with its attending proliferation of factories and water supply reservoirs, involves the progress of algal control. Further, the history of chemical compound syntheses and of laboratory techniques are interrelated with efforts to provide insecticides, weedicides and algicides.

Methods of algal control have been and still are principally chemical, but there are other procedures, some promising, some possibly useful but as yet impractical. Depending on circumstances, satisfactory control of superabundant growths of algae can be achieved by physical means. Rarely, blooms can be reduced by laboriously dragging and harvesting, involving screening and skimming.

As we realized early in the history of chemical control, enriched waters induce objectionable algal growths, especially of blue-green genera. Therefore water blooms have been controlled by the reduction or elimination of growth-promoting nutrients. This has been done mostly by diverting nutrient-bearing inlets and sewage plant effluents. But some success may be achieved by chemically modifying water chemistry of algal habitats.

Another class of control measures is biological, involving several technicalities and processes, largely experimental but with possibilities. It has been suggested that voracious plankton predators such as the fish Gizzard Shad be introduced to troubled habitats to act as a natural deterrent to algal blooms. Other efforts involve modifications of fish populations and of microfauna which possibly might impose restrictions of algae by changing the food chain. Further, the development of cyanophages, viruses and antibiotics have been considered as measures to be used in conjunction with chemical treatments.

It is beyond imagination what the users of domestic water endured before the days of purification and control of tastes and odors. Judging from the literature, no complaints are registered in western countries in recent centuries, and yet the occurrence of algal blooms and disagreeable tastes were prevalent. Recognition of water blooms and water discoloration dates from early times, especially as judged from references in British literature. Perhaps the earliest written record of water blooms, however, is that of Pliny (Bostock & Riley Transl. 1855). Of passing historical interest is a reference dating from the 12th Century by Giraldus Cambrensis (Ref. Mosheim 1863). J. E. Smith (1894) describes a bloom of "Conferva" in an Anglessy lake and Griffiths (1938) and Cooke (1890) report blooms dating from 1823. It is of interest also to note that sudden appearances of discolored water were attributed to forebodings or as responses to infamous acts, involving "miraculous powers" (Ref. Maxwell 1896 and Murray 1910). "Bloody" waters are frequently described in older literature, caused probably by blue-green algae or possibly by surface blooms of Euglena spp.

Apparently the urban populace of the civilized world was resigned to what in this day would be regarded as unacceptable drinking water. However, the algae involved in water blooms and in disagreeable tastes became taxonomically identified during the early 19th century, but attention to them was mostly limited to naming and to classification. It was not until much later that a causal relationship between algae and bad water tastes was established. In this country the role of algae was pointed out in 1876 by W. G. Farlow of Harvard University in his report on algae in the Boston water supply to the Cochituate Water Board.

Whatever bad tastes and odors algae may have contributed to water supplies, only charcoal and filters were employed prior to the 1800's. But during the 18th and 19th centuries literature indicates that algae must have been a considerable nuisance. In England blooms were referred to as "breaking of the meeres"; in France as "fleur d'eau"; in Germany as "Wasserbluthe." In this country conspicuous algal growths were and are called variously by "frog spittle," "water moss," or even insect excreta.

Efforts to improve water quality by algicides possibly might be said to have grown out of early aeration processes, and later by sterilization, although as S. H. Hutner wrote one time,"The electric light was not invented by attempts to improve on the candle. Nägeli (cir. 1849 and Ref. Anonymous 1925) was perhaps the first biologist to describe the cidal effects of copper on algae resulting from his culture experiments wherein he drew water from copper coil spigots that killed his plants. He calculated that 1 part per 50 million of copper in the water was algicidal.

The German Kröhnke later (1893) is credited with being the first to suggest that copper be used to purify water of bacteria. But during the greater part of the 19th century aeration, along with filtration, was the common and apparently the only method of improving water taste and odor. Whereas aeration was helpful, it obviously was not effective in eradication of algal tastes.

In 1883 potassium permanganate was used to purify water, and later, 1898, as a coagulant, whereas in 1902 it was applied as a cidal agent against both bacteria and algae. Again, in modern times Fitzgerald (1964) found potassium permanganate to be of limited value as an algicide because it is corrosive and because it leaves objectionable precipitants.

Ozone was suggested for sterilization of water as early as 1873, and 20 years later was used to neutralize tastes and odors. Chlorination for purification was used in Belgium in 1902 and then in England (1905-1908) where it was found to be also effective as an algicide, but with objectionable aftereffects. Disagreeable tastes and odors remain and many species of algae become immune. In this country F. E. Hale (1925, 1926, and 1927) of New York investigated and experimented with chlorine as an algicide and described results in his well-known papers.

The combination of chlorine and ammonia, known as chloramine, was discovered to be highly efficient as bactericidal agent in 1904, but curiously was not put into practical application until 1915. In this country cuprichloramine (chlorine & copper sulphate) was introduced later (1937).

The effectiveness of copper as an algicide, discovered by Nägeli was finally given practical application in France and Germany during the last years of the 19th century. Its success in Europe quickly spread to the United States where, according to literature, it was used by various sanitary engineers in the early 1900's. It was finally becoming realized that much of the objectionable qualities in drinking water were produced by algae, hence the drive to eradicate the cause rather than the effects. During the last part of the 19th century algal blooms had become more and more obnoxious. By 1878, according to Moore & Kellerman (1905), then of the U.S. Department of Agriculture, over 60 cities had registered troubles with algae in water supplies.

The use of copper sulphate by individual water supply engineers came to the attention of the Department of Agriculture, and by an act of Congress G. T. Moore and K. F. Kellerman were directed to experiment with and to test copper sulphate as an algicide and fungicide. For their work the Massachusetts Board of Health provided facilities and biological material. Results of scientific tests were presented and discussed at a symposium held by the New

England Water Works Association in New York wherein the ability of copper sulphate to kill microorganisms was described. Subsequently, the cidal value of copper sulphate, together with methods, dosage recommendations, and methods of application were presented in the papers of Moore (1902 and 1904), Moore and Kellerman (1904 and 1905), Moore and Goodnough et al. (1905).

Thus, having been publicized and given official recognition, copper sulphate became the standard algicide for general use, especially since it met all the requirements:

1. Successfully toxic to a great variety of algal species and at low concentrations.
2. Relatively easily applied.
3. Safe for fish and other aquatic animals.
4. Safe for human beings.
5. No objectionable side- or aftereffects (at least after the first day following treatment, none that cannot be eliminated by activated carbon).

For 25 years following its acceptance copper sulphate was used generally, having been regulated by a directive that its application should be conducted by authorized persons, and by permit. Apparently the first use of copper sulphate in Wisconsin occurred in 1918, but its application became popular and highly effective by the work of B. Domogalla. Here in the Madison lakes he carried on what might be called classic applications during the late 1920's, and later became internationally known through his patented copper alkanolamine salts or cutrine which he used both in this country and abroad.

The continued search for even better and cheaper algicides was implemented during and immediately after World War II by the United States biological and chemical research laboratories in Maryland. Many new chemicals were developed and synthesized, including pesticides and weedicides. Perhaps the war period marks the beginning of intensive search for algicides and of the development of means other than chemical for algal control.

We are indebted to C. M. Palmer, T. E. Maloney, and to G. P. Fitzgerald and coworkers who screened and tested many of these and other chemicals for algicidal properties. Fitzgerald (1959 and 1962) screened some 300 chemicals and results have been usefully summarized in a bulletin (Fitzgerald 1971) from the University of Wisconsin Water Resources Center. Further, Fitzgerald and coworkers have carried on exhaustive studies to test biodegeneration of copper sulphate and other algicides, and also their detoxification through absorption and/or precipitation. Methyl mercuric chloride, for example, was found to be not biodegradable whereas phenyl mercuric chloride was (is). Also, significant studies were made on the specificity of several algicides, providing useful information in determining appropriate concentrations. Fitzgerald found a large number of redox compounds to be effective against blue-green algae at concentrations varying from 1 to 20 ppm, but quinone compounds were found to be non-toxic. Perhaps the most promising of the agents tested proved to be

2,3-dichloronaphthaquinone which killed algal cells in 10 minutes at concentrations of 10 μg/l. This agent, known as Dichlone, was found to be non-toxic to green algae and aquatic weeds, however. But when applied as a spray it was found to be effective against blue-greens in concentrations of 30 to 35 ppb, even when blooms were extremely dense. Although Dichlone is effective at concentrations less than required for copper sulphate, it is, however, more selective and is not as overall effective against a variety of algae. Another chemical found to be highly selective against blue-green algae is phenanthraquinone.

Following the development and availability of post-war chemicals, Palmer and Maloney (1955) and Palmer (1957) screened some 56 for algicidal possibilities. Their reports divide the chemicals (including antibiotics) into 10 categories.

1. Inorganic salts, including mercuric chloride which is significantly not detoxified after application.
2. Organic salts, including natrium pentachlorophenate which is very irritating to the skin when used as an algicide in swimming pools; triethronolamine of copper; algimycin.
3. Organic acids.
4. Alcohol-ketones.
5. Substituted hydrocarbons.
6. Phenols.
7. Quaternary ammonium.
8. Amines and derivatives.
9. Rosin amine compounds. Rada; Monuron (used in Russia).
10. Antibiotics.

It is not appropriate to present herein a detailed review of numerous results of tests, but in summary, all the exhaustive experiments performed by Fitzgerald, Palmer, Maloney and others yielded a tremendous amount of information regarding the control of algae by chemical means during this period of algicidal history (1950's and 1960's).

Immediately after the war and during the last 25 years, chemical companies, through their own research or by using already tested substances, have prepared algicides for commercial dispensing under trade names. Perhaps the majority of these have been designed for swimming pools and aquaria--such as Algimycin-400; but Algimycin-PLLC is effective against pond and reservoir algae. After all these more recent studies, reports and developments, most of the chemicals are economically prohibitive for the treatment of blooms in lakes and large reservoirs.

But during recent times there has been increased attention toward the control of algae by means other than chemical. The sciences of limnology and phycology have come to provide many analyses which have emphasized biological-chemical interrelationships and ecological concepts. Accordingly, the problem of algal control has been subjected to highly sophisticated attentions. As mentioned earlier, attempts to develop algistatic methods, if not algicidal, have been recommended. Experimentally these show some promise, but are overshadowed by inabilities to receive financial support or official acceptance for civic purposes. Consequently many of the suggested or experimental control measures are mostly confined to private or individual research exercises, and include both physical and biological operations.

One aspect of biological control involves the use of phages. As long ago as 1963 parasitic phages of blue-green algae were discovered, first by Safferman and Morris and named LPP-1, so called because of the first initial of the generic names of the algae parasitized. Cyanophages have been found to occur rather generally and to be widely distributed, especially in sewage lagoons. Shilo (1971), Safferman _et al_. (1969a and b), Daft _et al_. (1970), Padan _et al_. (1967), as well as other workers have added much to our knowledge of the biology of phages and their specificity as parasites. Results of their work offer many possibilities and it is likely that future research may yield some effective, natural means for treating objectionable algae. Thus far the high selectivity of phages and the ability of some species to develop immunity are problems which must be overcome if they are to become suitable algicides. Unfortunately, thus far no phages are known which will attack toxic species of blue-green algae. Since phages are so widespread in nature it is obvious, nevertheless, that they do not exert any appreciable control over algal blooms. This suggests that another problem is that of mass production of cyanophages for successful applications against algal blooms.

Another area of research into algicides which until now offered little application is that of bacterial parasitism and antibiotics. More and more is being learned about the antagonism of one species of algae toward others through extrametabolites. D. O. Harris (1970, 1971a and b) and Harris and Parekh (1974), among others, have made exhaustive tests of the inhibitory properties of several species of algae. Like cyanophages, antibiotic reactions are highly specific.

Biological control through the radical modification of the aquatic environment such as changing the biota, the food chain, or by starvation have been suggested. Many recent and current studies have pointed up the successes of these rather involved measures--measures mostly experimental and without any sound basis for judgement as to their long-range performance.

A method of algal control which is practical and which has been tried lies within what might be termed starvation. The diversion of nutrient-bearing inlets and sewage plant effluents has had positive results in such places as the Madison, Wisconsin lakes, in Iowa lakes, Lake Washington at Seattle, and lakes in Sweden. The reduction, especially of phosphorus and nitrogen eventually reduces the development of superabundant algal floras. And the reduction of nutrients through tertiary treatments in sewage plants has had successful, practical results in algal control.

Recently, May (1974) and May and Baker (1978) found that by using ferric alum the available phosphorus was depleted to the extent that populations of Anacystis cyanea were significantly reduced.

Thus, the progress of algal control methods has reached a stage in which a variety of techniques are being explored. But at present chemical methods are still the most successful and practical, and among these copper sulphate applications in lakes and reservoirs are the most reliable and the least expensive.

REFERENCES

Anonymous. 1925. How the effect of copper sulphate on algae was discovered. Eng. Contract. 64:283.

Cooke, M. C. 1890. Freshwater algae. London. 1890.

Daft, M. J. F., J. Begg, and W. D. P. Stewart. 1970. A virus of blue-green algae from fresh water habitats. New Phytol. (In Press 1970).

Farlow, W. G. 1876. Reports on peculiar conditions of the water supplied in the city of Boston. Rep. of the Cochituate Board. 1876.

Fischer, A. 1884. Über das Vorkommen von Gipkristallen bei den Desmidiaceen. Jahbr. Wiss. Bot. 14:133-184.

Fitzgerald, G. P. 1959. Bacterial and algicidal properties of some algicides for swimming pools. Appl. Microbiol. 7:205-211.

Fitzgerald, G. P. 1962. Bioassay for algicidal chemicals in swimming pools. Water & Sewage Works. 109:361-363.

Fitzgerald, G. P. 1964. Factors in the testing and application of algicides. Appl. Microbiol. 12:247-253.

Fitzgerald, G. P. 1971. Algicides. Univ. Wisconsin Water Res. Center. Lit. Rev. No. 2:1-50.

Hale, F. E. 1925. The use of copper sulphate in the control of microscopic organisms. Phelps Dodge Corp. New York. 44 pp.

Hale, F. E. 1926. Algae treatment of reservoirs. Jour. Amer. Water Works Assoc. 16:765-768.

Hale, F. E. 1927. Algae treatment of reservoirs. Water Works Eng. & Contract. 66:83-84.

Harris. D. O. 1970. An autoinhibitory substance produced by Platydorina caudata Kofoid. Plant Physiol. 45:210-214.

Harris, D. O., 1971a. A model system for the study of growth inhibitors. Arch. f. Protistenk. 113:230-234.

Harris, D. O. 1971b. Growth inhibitors produced by the green algae (Volvocaceae). Arch. Mikrobiol. 76:47-50.

Harris, D. O. and M. C. Parekh. 1974. Further observations on an algicide produced by Pandorina morum, a colonial green flagellate. Microbios. 9:259-265.

Kröhnke, B. 1893. Suggestions for the improvement and sterilization of surface waters by chemical methods, with special reference to the Elbe water at Hamburg. Jour. f. Gasbeleuchtung u. Wasserrersorgung. 36:513. (Deutsch.)

Maxwell, H. 1896. County History, Scotland. 2. Dumfrieschire.

May, V. 1974. Suppression of blue-green algal blooms in Braidwood Lagoon with alum. Jour. Australian Inst. Agric. Sci. 40:54-

May, V. and H. Baker. 1978. Reduction of toxic algae in farm dams by ferric alum. New South Wales Dept. of Agric., Tech. Bull. 19:1-16.

Moore, G. T. 1902 (1903). The contamination of public water supplies by algae. Yearbook, Dept. Agric. 1902:175-186.

Moore, G. T. 1904. A new method for the purification of water supplies. Amer. Jour. Pharm. 76(12):553-564.

Moore, G. T. and K. F. Kellerman. 1904. A method of destroying or preventing the growth of algae and certain pathogenic bacteria in water supplies. U.S. Dept. of Agric., Bur. Plant Indust. Bull. 64:1-44.

Moore, G. T. and K. F. Kellerman. 1905. Copper as algicide and disinfectant in water supplies. U.S. Dept. Agric., Bur. Plant Indust. Bull. 76. 55 pp.

Moore, G. T. and X. H. Goodnough et al. 1905. A symposium on the use of copper sulphate and metallic copper for the removal of organisms and bacteria from drinking water. Jour. N. E. Waterworks Assoc. 19(4):474-582.

Mosheim, L. 1863. Ecclesiastical History. (Ed. W. Stubbs).

Murray, J. 1910. Bathymetrical survey of Scottish freshwater Lochs. I. Edinburgh. 1910.

Padan, E., M. Shilo, and N. Kislev. 1967. Isolation of cyanophages from freshwater ponds and their interaction with Plectonema boryanum. Virology 32:234-246.

Palmer, C. M. 1957. Evaluation of new algicides for water supply purposes. Taste & Odor Control Jour. 23(1):1-4.

Palmer, C. M. and T. E. Maloney. 1955. Preliminary screening for potential algicides. Ohio Jour. Sci. 55(1):1-8.

Pliny. Natural History. (Transl. Bostock & Riley, X. 1855, p. 493).

Safferman, R. S. and M. E. Morris et al. 1969a. Serological and electron microscope characteristics of a new group of blue-green algal viruses (LPP-2). Virology 39:775-780.

Safferman, R. S. and I. R. Schneider et al. 1969b. Phycovirus SM-1: a virus infecting unicellular blue-green algae. Virology 37:386-395.

Shilo, M. 1971. Biological agents which cause lysis of blue-green algae. Mitt. Intern. Ver. Limnol. 19:206-213.

Smith, J. E. 1894. English Botany. London. 1894.

SELECTIVE ALGICIDES

by

George P. Fitzgerald
ALGAE ACRES
3644 Rivercrest Rd.
McFarland, Wis. 53558

ABSTRACT

The various problems caused by algae are presented and evaluations made of the chemicals most suited for their control in fish ponds, water reservoirs, lakes, small ponds, and swimming pools. The advantages of chelated copper products over inorganic copper sulfate are discussed and results of tests of the comparative effectiveness of various commercial products are presented. Emphasis is on the evaluation of various algicides for particular algal problems by simple testing procedures. The need for biodegradation studies of chemicals used to control algae is also pointed out.

INTRODUCTION

The use of selective algicides to control obnoxious growths of algae makes multiple uses of bodies of water possible. Although it would be preferable to prevent algae problems by control of nutrients or environmental manipulations, we must control the problem first while other solutions are developed. However, the mere presence of algae should not be looked upon as a problem requiring solution. It should be remembered that in order to get the greatest growth of desirable fishes in fish ponds, as well as make it easier to harvest the fish, fish farmers are instructed to maintain an algal bloom such that their fingers cannot be seen through 30 cm of water. Therefore all algal growths are not undesirable just because they are present. Obviously algae do cause problems in fish ponds such as when filamentous forms predominate and nets used to harvest the fish crop become fouled. This has also occurred in fertile bays of Lake Superior where growths of filamentous diatoms made fishing nets so heavy they could hardly be raised. The desirable species of algae for fish ponds seems to vary depending upon the area of the world and fish species raised but the preferred algae are palatable species which produce readily available organic matter for fish food organisms and remain suspended throughout the water column to produce oxygen at all levels. Thus blooms of floating planktonic blue-green algae usually require control because they do not appear to be very palatable and produce oxygen only in the surface waters, allowing bottom waters to become oxygen-deficient and cause fish kills. In some areas of the world enough information is available so the proper kinds and amounts of fertilizers can be used to control the species of algae in fish ponds. In this country copper sulfate and other selective chemicals have been used successfully to get rid of undesirable kinds of algae.

Relatively light growths of certain types of algae, such as Synura, can cause large problems in water reservoirs because of the production of obnoxious tastes and odors. In addition, mucilaginous coated algae can clog water treatment plant filters. The problems of massive growths in lakes of planktonic bloom-producing algae are obvious when one considers that they are 50% protein and may concentrate downwind in decomposing layers 10 to 20 cm thick.

Historically, copper sulfate has been successfully used to control or prevent such obnoxious growths of algae. In fertile waters the consequence of treatments with copper sulfate is that sometimes green algae more resistant to copper replace the original bloom organisms (Kocurová, 1966). This shift in algal species may be beneficial or it may create new problems, such as when a filamentous green alga, Hydrodictyon (waternet), develops in vast floating patches. Thus, highly specific algicides applied to fertile waters may be used to cause an algal species change. This is a natural shift because when the original bloom organisms are killed, there would be an increase in available organic matter which results in increased bacterial numbers and a consequential increase in CO_2 generation. Algae favored by higher CO_2 concentrations or lower pH values would be the most likely organisms to develop under these conditions.

The uncontrolled growth of filamentous green algae in lakes, ponds or canals can cause problems ranging from unesthetic repugnant green scums, such as caused by Spirogyra (frog spittle), to cause the closing of beaches because of extensive accumulations and subsequent decay of growths of Cladophora or impeding navigation on rivers or canals when massive growths of Pithophora accumulate. There has been some success in the control of such obnoxious algae in smaller ponds and lakes by encouraging balanced growths of aquatic weeds and desirable amounts of algae, but on larger bodies of water the physical collecting and hauling away of accumulated algal debris has been necessary. Toxic organic chemicals such as rosin amines, triazine derivatives, and acrolein as well as inorganic copper sulfate have been used to control these algae but there appears to be much more successful potential control by the use of chelated copper algicides.

The control of algae in swimming pools probably represents one of the main areas where copper products are not successful. The presence of algae in swimming pools indicates that bactericidal conditions have not been continuously maintained. This may cause esthetic problems due to algal growths in the water or on the floor and sides of pools as well as real problems of lack of visibility in deeper portions of pools and slippery floors or walks. Although copper products have been shown to prevent the growth of swimming pool algae, they do not kill these algae and we must use toxic organic compounds for their kill and control when toxic concentrations of the halides, chlorine or bromine, cannot be maintained.

Although we have methods for evaluating the efficacy of chemicals toxic to problem-causing algae, we must remember that the algae probably would not be a problem if the essential algal nutrients could be controlled. In infertile waters when an occasional algal bloom does appear and is killed with a toxic chemical, the nutrients that supported that algal growth will be released from the killed algae (Fitzgerald, 1970; Fitzgerald and Faust, 1967) and will be available for the growth of another crop of algae. In fertile environments where nutrients are not limiting when a bloom of algae is killed by toxic chemicals, the net result usually is that a new species or group of algae replaces the former problem algae (Muracova, 1967; Guseva, 1952; Fitzgerald and Skoog, 1954). With enough experience we may eventually be able to destroy obnoxious algal growths and encourage desirable algal species by the proper use of selective algicides.

The fact that when the presently used algicides are applied to control obnoxious algae the algae controlled or new forms of algae grow back in the treated water indicates that these products are removed from the water or are detoxified (biodegraded) by the algae controlled. The biodegradation of algicides or pesticides in general is a study of prime importance to anyone interested in protecting aquatic environments for normal multiple uses without interference from obnoxious growths of plants or animals. There is a definite need to demonstrate that chemicals used for the control of algae are safe for use in the environment.

EXPERIMENTAL METHODS FOR SELECTING ALGICIDES

The testing of chemicals for the control of algae should be designed to evaluate the effectiveness of the chemicals in killing or preventing the growth of algae and not to keeping laboratory or field personnel busy. It is essential to use simple procedures that can be readily repeated in order to evaluate the effects of different environmental factors without wasting time or laboratory space. The tests should be related directly to a particular field problem and therefore, the kinds of algae to be tested should represent those causing that problem. The medium in which the tests are carried out should have the general characteristics of pH, hardness and alkalinity that reflect the conditions under which the problem algae grow.

The algae causing problems in lakes and ponds have been found to be particularily sensitive to the toxicity of copper, whereas closely related species that do not normally become obnoxious under these conditions appear to be more resistant to copper. Thus, to evaluate potential algicides, the strains of algae used should be carefully chosen so they truly represent those actually causing the problem. Suitable species for testing are the planktonic bloom-forming cultures listed in Table 1a and filamentous green algae cultures listed in Table 1b. Stock cultures of these algae can be grown in Gorham's dilute alkaline medium (Hughes, *et al*., 1958), or in this medium plus 10% secondary sewage effluent. Gorham's medium consists of, in mg/L, $NaNo_3$, 496; K_2HPO_4, 39; $MgSO_4 \cdot 7H_2O$, 75; $CaCl_2 \cdot 2H_2O$, 36; $Na_2SiO_3 \cdot 9H_2O$, 58; Na_2CO_3, 20; Ferric citrate, 6; Citric acid, 6; EDTA, 1. In tests of the toxicity of copper the last 3 nutrients should be replaced with $FeCl_3$ (3 mg/L) since they affect the solubility of copper and EDTA reduces the toxicity of copper (Fitzgerald and Faust, 1963). The algae can be cultured in test tubes or 50 ml Erlenmeyer flasks at room temperature without shaking. Light intensities of 100 ft. C. or less are suitable. Consistently good growth can be attained when these algae are added to test media to give a final concentration equivalent to 1,000,000 cells/ml. This concentration of algae is such that the bottom of a lake would not be visible through 1 meter of water. Optical densities can be used instead of cell counts to measure concentrations of algae in stock cultures. Using 1 cm cells at 600 or 750 mu,an O.D. or absorbance of 0.3 is about equivalent to 25,000,000 cells/ml. Clumped or filamentous algae can be finely suspended for uniform measurements and inoculation by mixing in sterile Waring blenders for 1/2 to 1 min. Consistency must be maintained in the amount of algae used in comparing different algae or chemicals because the amount of toxic chemical required to prevent the growth of algae is related to the amount of algae present (Table 2) and not to the volume in which the algae are suspended (Fitzgerald, 1964).

The algae causing problems in swimming pools are usually blue-green algae, such as the "black algae" of California pools, *Phormidium inundatum* (Wis. 1093), but some green algae have also been isolated from problem pools, represented by *Chlorella pyrenoidosa* (Wis. 2005). These algae grow well in Allen's neutral medium (mg/L): NH_4Cl, 50; $NaNO_3$, 1,000; K_2HPO_4, 250; $MgSO_4 \cdot 7H_2O$, 513; $CaCl_2 \cdot 2H_2O$, 66; $FeCl_3$, 3. Algae can be cultured and tested in test tubes or 50 ml Erlenmeyer flasks at room temperature without shaking. Light intensities of 100 ft C. or more are suitable. Inoculations of these algae to final concentrations equivalent to 300,000 cells/ml are standard. Such concentrations in a swimming pool

Table 1. Lake and pond algae found suitable for algicide testing

A. Planktonic Algae

- Gleotrichia echinulata (Wis. 1052)
- Anabaena circinalis (Wis. 1038)
- Microcystis aeruginosa (Wis. 1036)
- Oscillatoria rubescens (Wis. 2000)
- Dictyosphaerium pullchellum (Ind. 70)

B. Filamentous Algae

- Hydrodictyon reticulatum (Ind. 515)
- Cladophora glomerata (Ind. 1484)
- Spirogyra sp. (Ind. 918)
- Ulothrix acuminata (Ind. 1178)

Table 2. The effect of cell density on the concentration of a copper product required to prevent the growth of Selenastrum capricornutum. AAM Medium, 18 days incubation (Fitzgerald, 1975).

Cell Density (cells/ml)	Concentration of Algimycin PLL-C[1] To be Algistatic (mg/L)
10,000	0.05
50,000	0.15
300,000	0.50
1,000,000	2.5

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1. Algimycin PLL-C - 5% Cu - Great Lakes Biochemical Co., Milwaukee, Wis.

would make the bottom invisible through 2 m of water.

Toxicity tests using laboratory cultures of algae are carried out by adding 6 to 8 increasing amounts of a toxic product to inoculated tubes or flasks and incubating the cultures in light. Usually after 2 or 4 days the untreated control cultures will show definite signs of growth and inhibited cultures can be distinguished visually. Therefore, at this time re-testing of selected concentrations of the products and variations in environmental factors can be started without waiting for the normal 7 to 10 days' incubation when final results are recorded. Concentrations of the tested chemicals should be reported that 1) cause no visible effects compared to untreated control cultures, 2) partially inhibit the growth of the alga, such as 50, 75 and 90% inhibition, and 3) are algistatic or prevent the growth of the alga. To be algicidal a treatment should kill algae. To determine if treated algae are dead, samples are removed to fresh sterile media and incubated for 7 to 10 days. If algae do not grow in the subculture, the concentration used was algicidal. Treatment times should be selected to represent the time a chemical could be expected to be available to algae under field conditions. The time could vary from a few minutes to 24 hours, but all competitive chemicals should be tested the same length of time.

The evaluation of the duration of the algistatic or algicidal properties of swimming pool chemicals under field conditions can be carried out by adding test algae to samples of swimming pool water collected at different times after the swimming pool was treated (Fitzgerald, 1962). Prior to the addition of the swimming pool chemical to be tested, a quantity of water is taken for later use in making dilutions. All water samples should be dechlorinated and fertilized with 1 mg/L of phosphorus as K_2HPO_4, 1 mg/L of iron as $FeCl_3 \cdot 6\ H_2O$, and 10 mg/L of nitrogen as $NaNO_3$. Swimming pool water samples of 5, 12.5, and 25 ml are tested for the presence of toxic chemicals, after dechlorination, by making the samples up to 25 ml with untreated pool water, adding the equivalent of 300,000 cells/ml of either Chlorella or Phormidium, and incubating for 7 to 10 days. Water samples with the same growth as untreated control samples would be considered to be nontoxic. Samples with no increase in growth from the inoculation concentration would be algistatic and samples with no algae would be algicidal. Results with the different volumes of treated swimming pool water give the efficacy of the swimming pool product at 25, 50, and 100% after the duration times tested. Thus, these procedures will test how long a product is effective under field conditions and give quantitative data as to use dilutions at which the product is still effective.

Specific algae causing problems in ponds or canals can be used to evaluate the relative effectiveness of toxic products even when laboratory cultures are not available.

Field algae readily tested are Cladophora, Spirogyra, Ulothrix, and Chara. Collections of algae can be made from the ponds to be treated and sufficient pond water should be taken as media for the tests. Algae can be stored in open beakers at room temperature for a few days or in a refrigerator for a week or more.

A reasonably uniform inoculum is essential to compare tests of all chemicals and concentrations. Samples of 10 mg (dry weight) have been found to be optimum for these tests. Preliminary dry weight measurements determine what 10 mg of the alga look like and then 20-40 piles are made that appear to have about this same amount of algae. These are added to treatment vessels (tubes or 50 ml Erlenmeyer flasks) and the amounts of products to be compared are added. All chemical stock solutions should be made in the water to be treated so the effect of that particular water on the efficacy of the products would be most evident. Treatment times should be uniform and of short duration (10 minutes for comparing the toxicity of sources of copper). After the treatment period the algae can be collected by using a forceps or pouring the water through a small plankton net. The algae are washed in running tap water for about 5 sec and transferred to tubes or flasks for incubation. After a few days the algae that have been killed by the treatments can be visually distinguished from unaffected algae by having turned from green to brown or having sunk to the bottom of the vessel. The amount of product required to kill 10 mg of a specific alga with a 10 min contact should be reported (Fitzgerald and Jackson, 1979).

Other methods can be used to determine if treated algae are killed by toxic chemicals instead of waiting the few days for the results to become visually obvious. One method requiring only overnight incubation and then testing whether the algae can absorb PO_4-P or the loss of extractable PO_4-P from the algae has been reported (Fitzgerald, 1974). Any method used to determine if the algae are dead should be made after the algae have been removed from the treatment solutions so toxic products will not interfere with the viability testing procedure used. The viability test method used should also be very simple and readily carried out because it is replacing visual observations after only a few days' time.

Chemicals used to control algae can be tested for detoxification (biodegradation) by simple modifications of algicidal or algistatic test procedures. If a toxic chemical added to an environment was not biodegraded by the action of the organisms present, the addition of a single dose of the chemical would be sufficient to maintain biocidal conditions. Thus, by reinoculating flasks after an alga has been killed by a toxic concentration of chemical and has had time to decompose, you can determine if the killed algae released the chemical in a toxic form. If the second addition of algae grow, that concentration of the chemical tested was biodegraded by the first algal inoculation. By testing different concentrations of chemicals with the second inoculation procedure you can find out how much chemical will be detoxified by a certain concentration of that algae.

LAKE ALGAE CONTROL

Historically copper sulfate ($CuSO_4 \cdot 5H_2O$) has been a successful algicide in lakes and reservoirs, destroying blooms of planktonic blue-green algae and diatoms with concentrations in reservoirs of 0.3 to 0.8 mg/L (Guseva, 1952). Copper sulfate can be readily applied to water bodies by methods ranging from dragging cloth bags of the crystals to aerial applications. In the low alkalinity waters of the Rocky Mountains copper sulfate is applied to irrigation canals on a continuous treatment basis resulting in the prevention of algae problems. However, many demands for algae control in lakes develop after the algal growths have become obnoxious and the amounts of algae present will determine the amount of chemical that must be applied. The chemistry of the water will also affect the effectiveness of copper sulfate applications since copper readily precipitates in alkaline waters. Thus any copper not immediately taken up by the algae is rapidly lost to the bottom of the lake or pond. It is for this reason that organic chelates of copper have been used to replace copper sulfate as an algicide. With proper chelation the copper is kept in solution and still toxic to the algae (Fitzgerald, 1963). Currently, two types of chelation of copper are used in commercial algicides, alkanolamines, such as triethylanolamine, and a mixture of citrate and gluconate of copper. All of these sources of copper will prevent the growth of algae (algistats) if they are maintained at toxic concentrations, but practical selection of the commercial product of choice should be based on which products will kill the algae the fastest with the least amount of copper and thus reduce the chance of side reactions with non-target organisms present in the environment. Comparative tests are readily carried out to evaluate which source of copper will be most effective in a particular water. Table 3 summarizes the results of laboratory tests to determine how much copper (mg Cu/L) was required to kill the planktonic bloom-forming blue-green alga, Microcystis aeruginosa, in an alkaline medium when 7 and 10 hour treatments were used (Fitzgerald, 1975). Copper from Algimycin PLL-C[1], a mixture of copper citrate and gluconate, was effective at lower concentrations than was copper from copper sulfate or Cutrine[2], an alkanolamine of copper. In tests of the relative amounts of copper required to kill filamentous green algae, such as Cladophora, Spirogyra and Zygnema with treatment periods of 1/4 to 1/2 hours it was found that from 1/2 to 1/10 as much copper was required when Algimycin PLL-C[1] was the source of copper as compared to copper sulfate and four

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1. Great Lakes Biochemical Co., Milwaukee, Wis.
2. Applied Biochemists, Inc., Mequon, Wis.

Table 3. The algicidal properties of different sources of copper against the blue-gree alga, *Microcytis aeruginosa* (Wis. 1036). 1,000,000 cells/ml in Gorham's Medium (-EDTA)
20 days' incubation. (Fitzgerald, 1975)

Percentage Inhibition of Growth of Subcultures With Different Concentrations of Copper (mg Cu/L)

Treatment Time (hours)	Copper Sulfate[1]		Cutrine[2]				Algimycin PLL-C[3]		
	0.1	0.2	0.05	0.087	0.1	0.2	0.05	0.087	0.1
7	0	75	0	0	0	75	90	100[4]	100
10	50	100[4]	50	75	90	100[4]	100[4]	100	100

1. $CuSO_4 \cdot 5H_2O$ - 25% Cu
2. Cutrine - 7.1% Cu - Applied Biochemists, Inc., Mequon, Wis.
3. Algimycin PLL-C - 5% Cu - Great Lakes Biochemical Co., Milwaukee, Wis.
4. Minimum algicidal concentration

commercial products (Fitzgerald, 1974; Fitzgerald and Jackson, 1979). Thus, all sources of copper are not equally effective against some problem-causing algae and evaluations should be made to determine the most effective product for a particular problem.

The need to use as little copper as necessary to control algal problems is particularly important when dealing with public-spirited ecology-minded persons. They would probably prefer the use of an organic algicide, such as 2,3-dichloronaphthoquinone, which was investigated as an alternative to copper sulfate (Fitzgerald and Skoog, 1954). This compound is very selective in that 5 species of planktonic blue-green algae were killed by concentrations of less than 5 ug/L but 100 ug/L or more were required to kill 15 other species of blue-green or green algae tested. Field tests indicated it was effective in controlling heavy blooms of blue-green algae, but it never became a popular algicide.

Another alternative to copper sulfate for the control of algae in lakes and water reservoirs has been potassium permanganate. This product is well known for its use in water treatment plants for controlling taste and odor problems in drinking waters. Although higher concentrations of potassium permanganate are required to kill planktonic blue-green algae (1/2 to 4 mg/L) than copper sulfate (0.05 to 0.1 mg/L), potassium permanganate may have an advantage because it kills some filter clogging green algae, such as Dictyosphaerium which are not killed by copper (Fitzgerald, 1966). Thus, potassium permanganate could be used when copper sulfate treatments caused a shift in algal species to obnoxious forms rather than those readily handled by normal water treatment processes.

Up until recent times the relative costs of various algicidal chemicals have favored the use of copper sulfate over more expensive products. With potential increases in the cost of copper it has become more essential to use as little copper as necessary for the control of algae and the more effective chelated forms of copper may be economic alternatives even in large bodies of water. In smaller bodies of water, such as ponds and canals, the cost of chemicals is of less importance than safety, ease of application and effectiveness of the products. Thus, some organic algicides have been found to be practical under certain circumstances. When rosin amine D acetate is handled carefully, it has had some success in the control of the filamentous green alga, Ulothrix, in fish ponds. Simple continuous treatments with rosin amine D acetate have caused this obnoxious alga to be replaced by a thin coating of diatoms which were a welcome change because they did not interfere with fish pond management as did the Ulothrix (Johnson, 1955). Substituted triazines, such as simazine, have been used for the control of the filamentous algae Hydrodictyon (waternet) and Zygnema in fish ponds.

With a concentration of simazine of 0.5 mg/L the undesirable algae were replaced by planktonic algae, but if these were also undesirable, a concentration of simazine of 2 mg/L would control all algal growths without affecting the harvest of bass-spawning ponds (Snow, 1963). Simazine is also used in the products, Aquazine[1], Algimycin GLB-X[2] and Algimycin 400[2], which have been found to be very effective in preventing the growth of algae in small ponds, ornamental pools and swimming pools. The substituted phenylureas, such as monuron and diuron, have also been found to be of value in preventing algal growths in fish aquaria and ornamental ponds. The triazines and phenylureas will probably increase in popularity when their algistatic properties are linked with algicidal chemicals to form commercial products that readily kill problem algae but also prevent growths of algae over long periods of time.

SWIMMING POOL ALGAE CONTROL

The bactericides, chlorine or bromine, can be used to control the growth of algae in swimming pools if high enough concentrations (0.5 mg/L) are maintained. The toxicity of these halides to algae are well established, but some species isolated from swimming pools have been shown to be relatively resistant. Chlorine must be present at all times in order to prevent the development of algal colonies on the walls or apparatus in a swimming pool because once massive layers of cells have developed the outer surfaces protect the inner layers from the oxidizing powers of chlorine. If chlorination is continuous but not uniformly distributed, colonies of filamentous blue-green algae, such as _Phormidium inundatum_, are selectively favored. When chlorination is only intermittent, any fast-growing alga could develop. Frequently the water is colored by growths of relatively resistant green algal species which are protected by mucilaginous coatings, such as _Chlorococcum_. Therefore, unless the proper level and distribution of chlorine is maintained throughout a swimming pool, the use of algicidal chemicals will be necessary.

Chemicals for use in swimming pools must be either algicides or long-lasting algistats. Because copper sulfate is only an algistat for the types of algae found in swimming pools and is readily lost from solution, this chemical is not effective in swimming pools. Silver products are also very effective as algistats but must be added frequently to maintain their effectiveness. Recently silver has been added to swimming pools by electrolytic processes or erosion feeders that continually replace silver lost by precipitation or detoxification. These processes are effective in maintaining algistatic, and bacteriostatic, levels in swimming pools, but weekly super chlorination (5 to 10 mg chlorine/L) treatments must be made to oxidize accumulated organic matter that can detoxify the silver (Fitzgerald, 1967). A recent alternative to super chlorination for removing organic matter is the use of a

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1. Ciba-Geigy Corp., Greensboro, N. Car.
2. Great Lakes Biochemical Co., Milwaukee, Wis.

commercial oxidizing product, Oxybrite[1], which can be added to pools without requiring swimmers to remain out of the water during the treatment. This product has also been used to generate bromine in swimming pools as an alternative to chlorination (Fitzgerald, Jackson and Stern, in preparation).

In contrast to the copper and silver products, quaternary ammonium compounds have been shown to be algicidal towards swimming pool algae. In order to be effective, though, these products must be present in algicidal concentrations for sufficient periods of time because they will not last long enough in swimming pool waters to be effective algistats (Fitzgerald, 1962 and 1971). The fact that the potential human pathogen, Pseudomonas aeruginosa, was found to increase in numbers in swimming pools treated with quaternary ammonium algicides and that this organism is resistant to relatively high concentrations of quaternary ammonium compounds leaves some doubt as to the advisability of using such products in swimming pools even under conditions in which they could be effective algicides.

The successful combination of an algistat, simazine, and an organic algicide in a commercial product, Algimycin 400[1], has demonstrated how products can be formulated to kill existing algal problems and to prevent algal growths in swimming pools. Table 4 summarizes data obtained when three types of swimming pool products were tested against the swimming pool alga, Phormidium inundatum (Wis. 1093). Two products contained copper, two products were quaternary ammonium compounds, and one product was a combination of a polymeric cationic compound and simazine. All but one of the products prevented the growth of Phormidium at concentrations of 8 mg/L or less. The copper-containing products were not algicidal at the highest concentration these products were tested, 8 mg/L. Related tests indicated that concentrations of 32 mg/L were also not algicidal. The two quaternary ammonium products were algicidal at concentrations 3 to 7 times those required to be algistatic. The simazine-containing product was algicidal at the same concentration required to prevent growth of this alga, 2 mg/L (Fitzgerald and Jackson, 1979; Fitzgerald, 1968). Thus, one can see that practical formulations containing both algistatic and algicidal chemicals are possible.

BIODEGRADATION OF ALGICIDES

There is a great need to determine if toxic chemicals added to aquatic environments could be potential environmental pollutants. In the case of algicides this can be readily tested by re-inoculating test vessels with the algae used. The results of different tests of this nature are summarized in Table 5 where different algae have been tested with increasing concen-

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[1] Great Lakes Biochemical Co., Milwaukee, Wis.

Table 4. Algistatic and algicidal properties of swimming pool chemicals against Phormidium inundatum (Wis. 1093). Inoculated at 300 000 cells/ml in Allen's medium. (Fitzgerald, 1971; Fitzgerald and Jackson, 1979).

Product	Concentration of Product (mg/L) To Prevent Growth of Algae	To Kill Algae
Swimfree[1]	>8[6]	>8[6]
Swimtrine[2]	8	>8[6]
Algistat[3]	4	28
Armazide[4]	2	6
Algimycin 400[5]	2	2

1. Swimfree - 7.1% Cu - Hydrology Labs., Inc., Smithtown, N.Y.
2. Swimtrine - 7.4% Cu - Applied Biochemists, Inc., Mequon, Wis.
3. Algistat - 50% Quats - Sears Roebuck and Co., Chicago, Ill.
4. Armazide - 36% Quats - Armour Pharmaceutical Co., Kankakee, Ill.
5. Algimycin 400 - 34% Polymeric cationic plus simazine - Great Lakes Biochemical Co., Milwaukee, Wis.
6. Highest concentration tested in these tests.

Table 5. The biodegradation of algicides. (Fitzgerald, 1975 and Fitzgerald and Jackson, 1979).

Algae	Product	Concentration of Product to Kill (mg/L) First Inoculation	Concentration of Product to Kill (mg/L) Second Inoculation
Spirogyra	Algimycin PLL-C[1]	1	4
"	Swimfree[2]	3	> 6
Selenastrum	Algimycin PLL-C[1]	0.5	5
Chlorella	Algaedyne[3]	10	> 160
"	1% Silver Nitrate	7.5	> 160
"	Mercuric chloride	0.5	2
"	Phenyl mercuric acetate	0.1	0.25
Phormidium	Cavco Algicide[4]	1	2
"	Black Algaetrine[5]	4	8

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1. Algimycin PLL-C - 5% Cu - Great Lakes Biochemical Co., Milwaukee, Wis.
2. Swimfree - 7.1% Cu - Hydrology Labs., Inc., Smithtown, N.Y.
3. Algaedyne - 0.8% Ag - U.S. Movidyne Corp., Chicago, Ill.
4. Cavco Algicide - 50% Quat. - Cavedon Chemical Co., Woonsocket, R.I.
5. Black Algaetrine - 53% Quat. - Applied Biochemists, Inc., Mequon, Wis.

trations of products to determine which concentration killed the original inoculum and which concentration was required when the flasks were re-inoculated with the same alga (Fitzgerald, 1975; Fitzgerald and Jackson, 1979). The two copper products were tested against field collections of Spirogyra and a laboratory culture of the green alga, Selenastrum. The silver, mercuric, and quaternary ammonium products were tested against the algae used to test swimming pool algicides. The toxicity of all of these chemicals and products was reduced by reactions with the target algae. The algae in some cases were also able to detoxify considerably more chemical than was required to kill the original inoculum. This has also been found when organic extracts of mud or dead algae were found to reduce the toxicity of practical algicides. Thus, the toxicity of the current algicidal chemicals is reduced by reactions with the algae they are used against. These results contrast with the fact that algal nutrients are released in available forms when algae are killed (Fitzgerald, 1970) and that one chemical, methyl mercuric chloride, has been found that was not detoxified by algae or fish (Fitzgerald, 1975). Therefore, all chemicals to be added to aquatic environments should be evaluated to determine if they will be biodegraded or remain in toxic condition to pollute the environment.

REFERENCES

Fitzgerald, G.P. 1962. Bioassay for algicidal chemicals in swimming pools. Water and Sew. Works. 109: 361-363.

Fitzgerald, G.P. 1963. Factors affecting the toxicity of copper to algae and fish. Proc. of Div. of Water and Waste Chemistry. A.C.S. meeting N.Y., N.Y. Sept. 8-13. p. 21-24.

Fitzgerald, G.P. 1964. Factors in the testing and application of algicides. Appl. Microbiol. 12: 247-253.

Fitzgerald, G.P. 1966. Use of potassium permanganate for control of problem algae. J.A.W.W.A. 58: 609-614.

Fitzgerald, G.P. 1967. The algistatic properties of silver. Water and Sew. Works. 114: 185-189.

Fitzgerald, G.P. 1968. Compatibility of swimming pool algicides and bactericides. Water and Sew. Works. 115: 65-71.

Fitzgerald, G.P. 1970. Evaluations of the availability of sources of nitrogen and phosphorus for algae. J. Phycol. 6: 239-247.

*Fitzgerald, G.P. 1971. Algicides. Literature review No. 2. U.S.D.I. Nat. Tech. Inform. Service P.B. 198130. 50 pp.

Fitzgerald, G.P. 1974. Shortcut methods test algicides. Water and Sew. Works. 121 (9): 85-87.

Fitzgerald, G.P. 1975. Are chemicals used in algae control biodegradable? Water and Sew. Works. 122: 82-85

Fitzgerald, G.P. and S.L. Faust. 1963. Factors affecting the algicidal and algistatic properties of copper. Appl. Microbiol. 11: 345-351.

Fitzgerald, G.P. and S.L. Faust. 1967. Effect of water sample preservation methods on the release of phosphorus from algae. Limnol. Oceanogr. 12: 332-334.

Fitzgerald, G.P. and D.F. Jackson. 1979. Comparative algicide evaluations using laboratory and field algae. J. Aquat. Plant Manage. 17: 66-71.

Fitzgerald, G.P. and F. Skoog. 1954. Control of blue-green algae blooms with 2,3-dichloronaphthoquinone. Sew. and Ind. Wastes. 26: 1136-1140.

*Gratteau, J.C. 1970. Potential algicides for the control of algae. Water and Sew. Works. (Reference No.) R24-R61.

---

* Literature Reviews

Guseva, K. A. 1952. Water bloom, its causes, prediction and control. Tr. Vses. Gidrobiol. Obshchestva Akad. Nauk SSSR, 4: 3-92. Nat. Res. Council of Canada Technical Translation 1068.

Hughes, E.P., P.R. Gorham, and A. Zehnder. 1958. Toxicity of a unialgal culture of Microcystis aeruginosa. Can. J. Microbiol. 4: 225-236.

Johnson, L.D. 1955. Control of Ulothrix zonata in circular ponds. Prog. Fish Cult. 17: 126-128.

Kocurová, E. 1966. The application of the algicide CA 350 in the Lubi Reservoir near Třebić, Czechoslovakia. Hydrobiolgia XVIII: 223-240.

Muracova, V. 1967. Biological investigations of an infiltration area and experiments with some algicides. Hydrobiologia 29(3/4): 505-646.

*Sladeckova, A. and V. Sladecek. 1968. Algicides-friends or foes? p. 441-458. In D. F. Jackson (ed.), Algae, man and the environment. Syracuse Univ. Press.

Snow, J.R. 1963. Simazine as an algicide for bass ponds. Prog. Fish Cult. 25: 34-36.

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*Literature Reviews

STATE-OF-THE-ART SUMMARY OF PHOSPHORUS INACTIVATION AS A LAKE RESTORATION TECHNIQUE

G. Dennis Cooke
Department of Biological Sciences
Kent State University
Kent, Ohio 44242

and

Robert H. Kennedy
U.S. Army Corps of Engineers
Environmental Laboratory
Vicksburg, Mississippi 39180

INTRODUCTION

Long-term control of or reduction in algal biomass in lakes can be achieved by significantly lowering the concentration of an essential nutrient. This can be accomplished by nutrient diversion, particularly if the lake is deep and flushes rapidly with water low in nutrients. The oft-cited case of Lake Washington (Edmondson, 1970) illustrates this approach. However in many eutrophic lakes, particularly those which are shallower, with extended periods of anoxic hypolimnia and well-developed littoral areas, extensive internal cycling of nutrients from sediments to the water column may occur. This process maintains concentrations of essential nutrients at levels sufficient to stimulate continued algal blooms, even after nutrient diversion (Cooke et al., 1977). Shagawa Lake, Minnesota (Larsen et al., 1975) is an illustration of this problem.

Most eutrophic lakes are small with the productive and regenerative portions in close proximity. Slow response to diversion may be the rule in these lakes and a second step, the control of some internal release, is required in order to achieve nutrient limitation. The addition of aluminum sulfate and/or sodium aluminate, is a lake restoration technique often called nutrient inactivation or precipitation. The purpose of this lake restoration procedure is to control lake phosphorus (P) concentration and thus accelerate improvement in lake trophic state after nutrient diversion. This paper briefly reviews this technique emphasizing representative case histories. A more detailed and complete review is found in Cooke and Kennedy (1980, in press).

ALUMINUM CHEMISTRY

Advanced wastewater treatment emphasizes nutrient removal. Here, iron, calcium, and aluminum salts have been considered for the precipitation of P. In lakes, only aluminum has received serious attention because aluminum complexes and polymers are inert to redox changes (in contrast to iron), are effective in entrapment and removal of inorganic and particulate P, and are of apparent low toxicity at the pH and dose needed to bring about lake improvement. Calcium additions are most effective at pH values above those found in natural waters (Stumm and Morgan, 1970).

When aluminum salts are added to water a series of pH-dependent hydrolyses ultimately form colloidal aluminum hydroxide, an amphoteric molecule which forms complex ions with other molecules and which polymerizes. A decrease in pH and total alkalinity occurs. The distribution of hydrolyzed aluminum species is pH-dependent, with polymerized $Al(OH)_3$ floc predominating between pH 6 and 8, aluminate ion above this range, and Al^{+3} below pH 4 (Figure 1). Reactions with phosphorus include the formation of $AlPO_4$, sorption of phosphates to the surface of aluminum hydroxide floc or

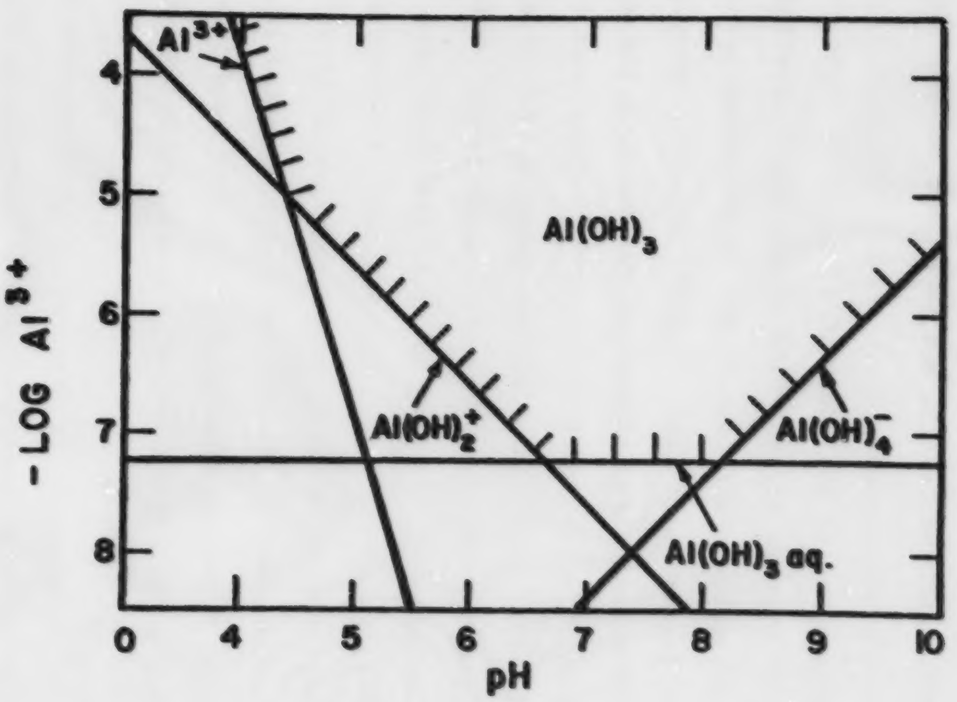

Figure 1. Solubility of amorphous hydroxide (from Eisenreich et al., 1977).

polymers, and by entrapment/sedimentation of particulate matter by the floc. Further details are found in Eisenreich et al. (1977), Burrows (1977), and Cooke and Kennedy (1980, in press).

Two approaches to the addition of aluminum salts to lakes for the purpose of achieving phosphorus limitation have been attempted. Nineteen of the 28 published accounts of aluminum treatment of lakes in North America, Europe, and Australia have emphasized phosphorus removal from the water column (e.g., S. A. Peterson et al.,1974). Here dose is determined in jar tests in which the aluminum salt is added until the desired degree of P removal is achieved. Total amount to be added to the lake is calculated from lake volume and total P content. Usually additions of aluminum are so small that little pH change and appearance of dissolved aluminum occurs. With this approach, little regard is given to control of P release from anoxic sediments, and in many cases little long-term control of P concentration has been achieved.

The second approach to lake treatment emphasizes the application to the sediments of as much aluminum as possible, within limits imposed by environmental safety, in order to achieve long-term control of the P released to the water column during anoxic periods and when groundwater seeps into the lake. This type of treatment is exemplified by the work of Cooke et al. (1978) and Kennedy (1978). Dose is determined by pH and by changes in dissolved aluminum concentration. Aluminum sulfate (alum) is the most frequently employed salt for lake treatment. When it is added, hydroxide is formed and pH falls. In the range of pH 7.0-5.5 dissolved aluminum concentration, a potentially harmful metal, is minimal. As pH and alkalinity continue to decrease with further addition, dissolved aluminum increases exponentially. Kennedy (1978), and later Cooke et al. (1978) defined the maximum dose as that pH at which no more than 50 µg Al/l was found, a concentration which Everhart and Freeman (1973) found to be safe for rainbow trout (Salmo gairdnerii). This dose can also be defined as that amount which reduces pH to 6.0 (R. H. Kennedy and G. D. Cooke, in prep.).

The amount of aluminum which can be added is directly related to lake alkalinity and thus varies from lake to lake. For soft water lakes, exemplified by the work of Dominie (1978), a mixture of aluminum sulfate and sodium aluminate is added, calculating how much of each is needed to maintain a pH at which dissolved aluminum will not increase.

The addition of aluminum for the purpose of controlling P release from sediments is the approach of choice for control of algal biomass, and P removal should be reserved for special applications.

ALUMINUM APPLICATION PROCEDURES

Aluminum salts have been applied, in both surface and hypolimnetic treatments by barge. Tanks on the barge are filled from shore by hoses and the material is mixed with water, by an on-board pump, on its way to a wide (5-10 m) manifold trailing behind or below the craft. Usually the area to be treated is marked by buoys and divided into areas. The total amount for each area is provided to the operators and gauges on the tank are used to estimate amount delivered. Details of several delivery systems are described in Cooke and Kennedy (1980, in press), and also in Kennedy (1978) and Cooke et al. (1978).

SELECTED CASE HISTORIES

A great deal of variability in procedures exists among the 28 reported cases (see Cooke and Kennedy, 1980, in press) of phosphorus inactivation/precipitation. This reflects the newness of this technique (1968-1980). Success has also been highly variable, ranging from failure to 4 years (longest reported monitoring period) of improved lake trophic state. Five lake treatments are briefly reviewed below, illustrating the range of procedures.

HORSESHOE LAKE, WISCONSIN

Horseshoe Lake is a small (9 ha), deep (Z max = 16.7 m; $\bar{Z}$ = 4 m), dimictic lake in Manitowac County, Wisconsin. This lake had the first reported phosphorus precipitation in the United States (J. O. Peterson et al.,1973). Blue-green algal blooms, dissolved oxygen depletions, and fish kills were attributed to the loading to the lake from domestic, agricultural, and industrial (dairy wastes) discharges. In May, 1970, 10.2 metric tons of liquid aluminum sulfate were applied by barge to the lake surface to precipitate phosphorus. Three barges were used, each with a holding tank for mixing dry alum with water, a pump, and an application manifold. Alum was pumped from the tank into the manifold, a perforated pipe which trailed the barges and was oriented perpendicular to the path of travel. The lake surface was divided into areas marked with buoys, and a pre-determined amount added to each area. This application plan has been followed for nearly all subsequent applications, with the exception that in most cases liquid alum is purchased rather than mixed at the lake site.

After treatment hypolimnetic (Figure 2) and epilimnetic total P concentrations were lower than before, although hypolimnetic P has increased slightly every year (up to 1978), according to J. O. Peterson (personal communication). Transparency increased, blue-green algal blooms in 1970 were reduced and there were no fish kills through 1972. No detrimental effects to benthic insect larvae were observed in surveys through 1978 (R. Narf, 1978).

This was a successful treatment despite the apparent rather small dose.

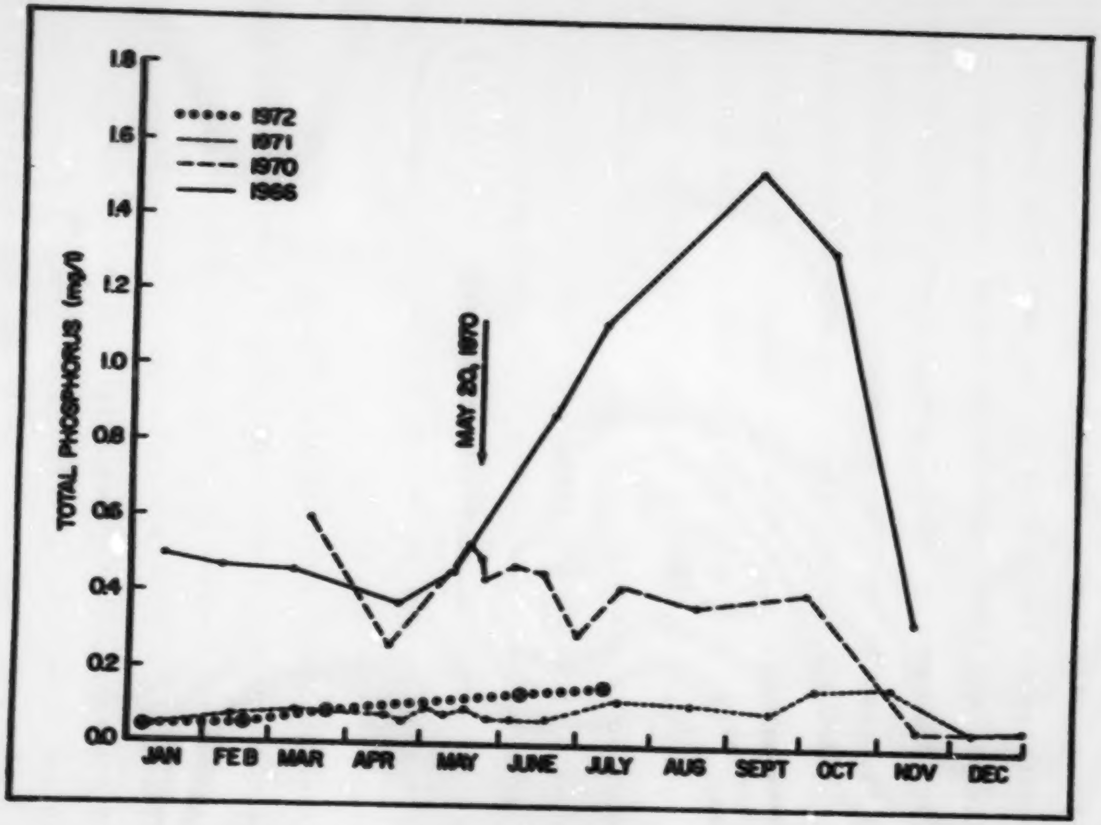

Figure 2. Hypolimnetic total phosphorus concentrations in Horseshoe Lake, Wisconsin (from J. O. Peterson et al., 1973).

WEST TWIN AND DOLLAR LAKE, OHIO

The limnological features of these lakes and details of their alum treatments have been described elsewhere (Cooke et al. 1978; Cooke and Kennedy, 1978; Kennedy, 1978). Dollar Lake is a small (2.2 ha), dimictic, eutrophic, alkaline bog, located in the Twin Lakes (Portage Co., Ohio) Watershed. The lake exhibits symptoms of severe cultural eutrophication, including blue-green algal blooms and hypolimnetic dissolved oxygen depletions. Carlson's (1977) TSI index was about 65 in 1973. In July 1974, 9 tons of liquid alum were added to the hypolimnion and 1 ton to the surface. Dose was based upon alkalinity and defined in accordance with procedures described in the section on aluminum chemistry. Alum was pumped from an on-shore tank through a hose floating on the lake surface to an anchored platform. The barge returned to the platform, filled a 275 gallon tank, proceeded to a previously marked section of the lake over the hypolimnion and added the alum to the 3 M contour via a 7 M wide manifold.

West Twin is a dimictic, culturally eutrophic (macrophytes, blue-green algae, hypolimnetic oxygen depletions) lake which is 35 ha in area, 4.3 M in mean depth, and with a maximum depth of 11.5 M. West Twin was treated in July, 1975 with 100 tons of liquid alum, all added to the 5 M contour in a dose which accorded with the definition for maximum dose (see aluminum chemistry). Final average dose for

Dollar was 20.9 gms Al/M^3, and 26 gms Al/M^3 for West Twin. East Twin, a downstream lake of identical limnological and cultural history, and with very similar features to West Twin, served as a reference lake. Application techniques were identical to those of Dollar except that two barges were used. The purpose of the treatments was control of P release from anoxic hypolimnetic sediments.

Figures 3 and 4 illustrate the change in the P contents of the lakes. In both, P content fell precipitously and has remained low through 1978, although Dollar exhibited signs of increasing P content in 1978. Internal P release in West Twin, calculated by a nutrient budget method (Cooke et al. 1977) was not completely controlled. Earlier experiments (Kennedy and Cooke, 1974; Kennedy, 1978) indicated that the aluminum hydroxide floc was effective in controlling much of the release, suggesting that the small but continued internal P release after treatment was littoral in origin. In both treated lakes, cell volume and blue-green dominance decreased and transparency increased.

The Carlson (1977) Trophic State Index (TSI) was used to evaluate the effect of the treatment in controlling algal biomass. The index represents change in algal biomass, as estimated from the relations between biomass and Secchi Disc transparency, chlorophyll, and total P, with each change of 10 units (e.g., from 60 to 50) representing a halving or

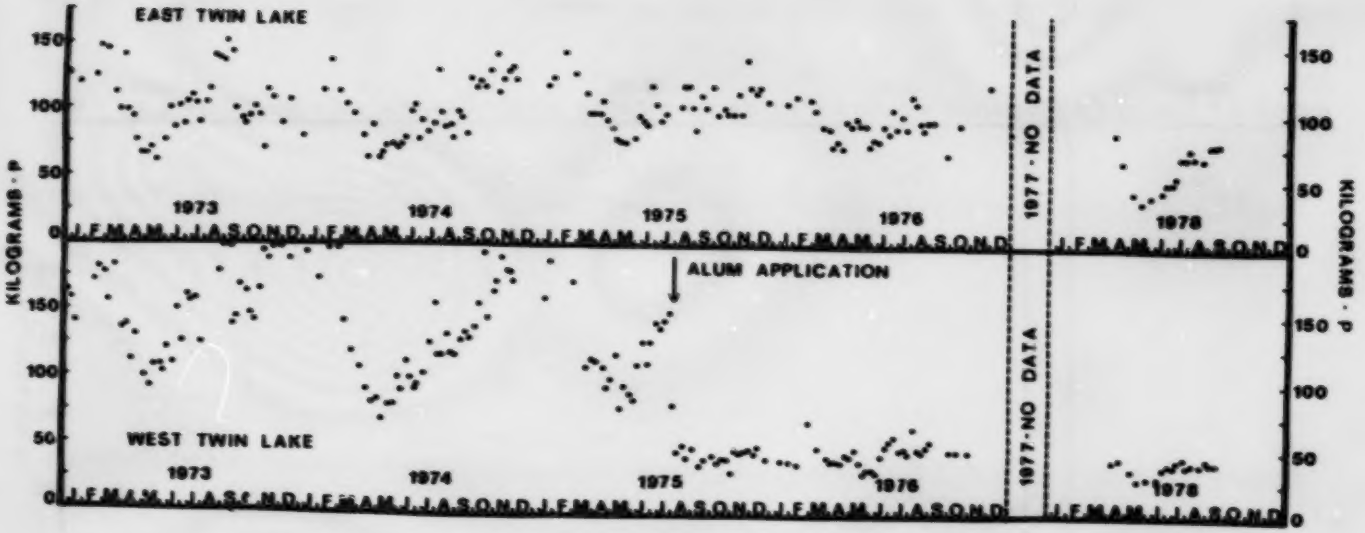

Figure 3. Phosphorus content of East and West Twin Lakes (from Cooke, 1979).

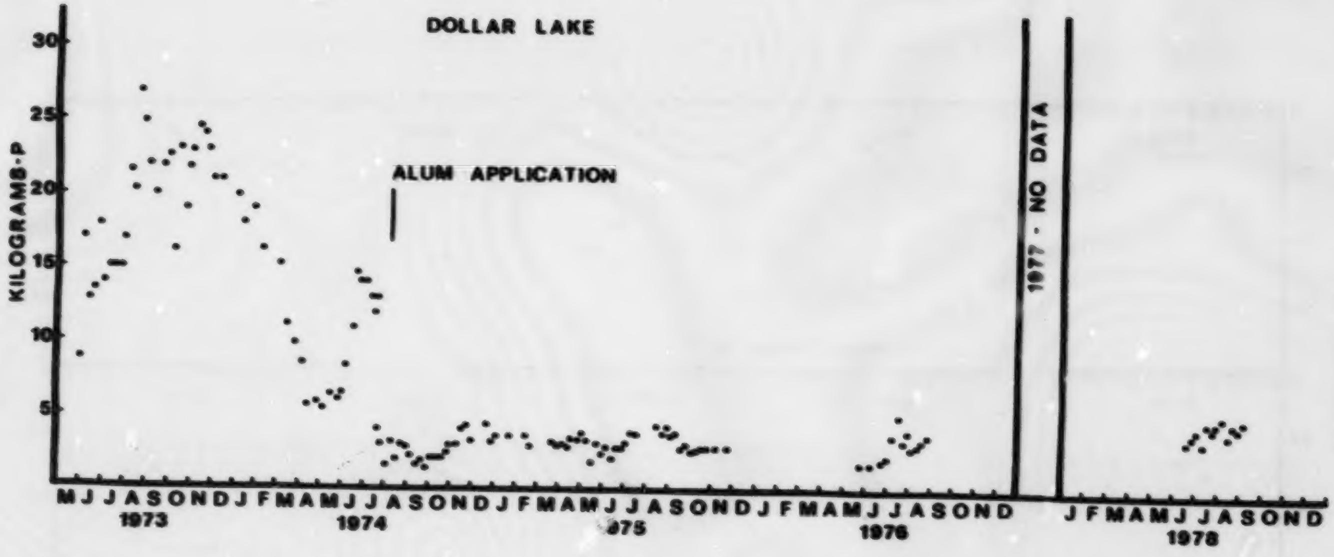

Figure 4. Phosphorus content of Dollar Lake (from Cooke, 1979).

doubling of biomass. Carlson (1979) judged the boundaries of mesotrophy to be 41 to 51. The responses of the lakes are listed in Table 1. Obvious and lasting (4 years) improvements in trophic state occurred. In 1979 a much greater than usual growth of rooted macrophytes took place. This response seems to be associated with the improved water clarity. The reference lake (East Twin) also improved after 1976 due to the influx (about 50-70% of water and P budget) of water low in P from West Twin.

MEDICAL LAKE, WASHINGTON, AND ANNABESSACOOK LAKE, MAINE

These lakes are considered together because they represent very high (Medical) and low (Annabessacook) alkalinities and thus significantly different approaches to aluminum dose. Medical Lake is a eutrophic, dimictic, seepage lake (64 ha, Z max 18 M, $\bar{Z}$ 10 M, with an alkalinity of about 750 mg/l as $CaCO_3$). A large dose was shown by jar tests to be needed for P removal, and it was determined that multiple surface and hypolimnetic treatments would be needed. In 41 days in summer 1977, 936 metric tons of liquid alum (12.2 gms Al/M^3) were applied for P removal, including 4 surface and 7 hypolimnetic applications. Dissolved oxygen conditions improved after treatment to the point where the lake could support a rainbow trout fishery. Total P fell from an average of about 300 µg P/l to about 60 µg P/l, and algal biomass was greatly lowered,thus improving transparency. The treatment

Table 1

Mean (May-September) Carlson Trophic State Index (from surface measures; adapted from Cooke, 1979), based on Total Phosphorus

	West Twin	East Twin	Dollar
1971	57.58	53.68	no data
1972	62.75	58.91	no data
1973	61.36	56.48	64.31
1974	59.84	58.89	no data
1975	55.85	57.14	50.22
1976	52.36	56.62	50.65
1978	44.25	47.27	47.79
1971-1974	60.38	56.99	64.31
1976-1978	48.31	51.95	49.55
decrease in algal biomass 1971-74 vs. 1976-78	2.41	1.01	2.95

at Medical Lake also shows that the period of treatment can be extended over many days (Gasperino and Soltero, 1978).

Annabessacook Lake, a soft (20 mg/l as $CaCO_3$) water, eutrophic lake, receives about 85% of its total P income from seepage (Dominie, 1978). The objective of the treatment was to control this source. In order to maintain pH at near normal levels, and thus to minimize the appearance of dissolved aluminum, while at the same time adding enough aluminum to control P release, a mixture of aluminum sulfate and sodium aluminate (1:1.6) was added to the hypolimnion (121 ha) in August, 1978. The 8-10 M contour received a dose of 25 gms Al/M^3, and the 10 M contour and below a dose of 35 gms Al/M^3, using an application system similar to earlier workers except that a segregated dual injection system was employed to prevent precipitation of aluminum salts in the manifold. Preliminary studies indicate lake improvement.

BRAIDWOOD LAGOONS, NEW SOUTH WALES, AUSTRALIA

Ponds also have severe problems with nuisance algae. May (1974) added liquid alum, along with suspended blocks of ferric alum, to control toxic blue-green algae in farm dams. The objective of the treatment was to control P release from sediments. A dose of 10.6 gms Al/M^3 and 31 gms Fe^{+3}/M^3 was added. Blooms of *Anacystis cyanea* and *Anabaena circinalis* were controlled, illustrating the effective use of P inactivation in shallow, circulating ponds.

TOXICITY OF ALUMINUM TREATMENTS

Burrows (1977) reviewed the toxicity of aluminum to aquatic biota. The data are sparse, particularly because many investigators failed to realize that the concentration of dissolved aluminum in test waters is pH-dependent. Some waters could receive very large amounts of aluminum before dissolved aluminum appeared at concentrations sufficient to induce toxicity.

Three laboratory studies are of value. Biesinger and Christensen (1972) found that Daphnia magna has a 16% reproductive impairment at 320 μg Al/l. Freeman (1973) and Everhart and Freeman (1973) report that a concentration of 5200 μg Al/l, whether at pH 9.0 where it is highly soluble or at pH 7.0 where it is nearly insoluble, seriously disturbed rainbow trout (Salmo gairdnerii) if present longer than 6 weeks. At 52 μg Al/l, there were no obvious effects on growth or behavior, leading Kennedy (1978) and Cooke et al. (1978) to adopt this value as the upper safety limit for dissolved aluminum in lake treatments. S. A. Peterson et al. (1974) found that Chinook salmon survived a dissolved aluminum concentration of 20 μg Al/l, and that D. magna did not reach a 96 hr TL_m with concentrations up to 80 μg Al/l.

In the field, several investigators report an apparent absence of toxicity to fish (Cooke et al. 1978; Bandow, 1974; Sanville et al. 1976) after lake treatments. Narf (1978) monitored Horseshoe, Pickerel, and Snake Lakes, Wisconsin, the earliest aluminum treatments in the United States, and found no negative impact to the benthic invertebrates living in them.

Moffett (1979) found a significant decline in species diversity of planktonic microcrustacea in West Twin Lake, Ohio, when comparing post-treatment diversity to both pre-treatment values and to the untreated reference lake. The cause of this diversity change is unknown.

RESEARCH NEEDS

This technique for lowering P concentration to the point of exerting control of algal biomass appears to be a successful one. Because nearly all of the treatments have been recent ones, almost no long-term monitoring of effects is available. This is a general problem with all lake restoration techniques and represents one of our most serious gaps in support of lake restoration research. Unless this type of support becomes available, meaningful cost-benefit analyses, a second serious gap in our knowledge, will be difficult or impossible. It is critical for the lake manager or citizen association to know the duration of effectiveness versus initial cost.

Duration of effectiveness may be related to aluminum dose, but this is not known. The difference between a dose for P removal and the "maximum" dose defined by Kennedy

(1978) (see aluminum chemistry section), in terms of controlling P release from sediments, is clear. We do not know how long that maximum dose will continue to sorb P, although it appears that effectiveness at Dollar Lake (Figure 3) is declining after 4 years. If both aluminum sulfate and sodium aluminate were added simultaneously, pH would be kept in a range in which very little dissolved aluminum would appear. In that case, one could presumably add as much aluminum as affordable. Would duration of effectiveness in controlling P release be increased in proportion to dose?

Application procedures with a barge are costly and can be slow and awkward. Alternative means of application should be sought, including consideration of the application by high velocity hoses from shore to lake surface.

Toxicity problems, with the possible exception of the diversity change in planktonic microcrustacean at West Twin Lake, have not appeared. Yet, we know almost nothing of the impact of the treatment upon the actual level of biological organization to which it is applied. Nearly all toxicity studies have been to monospecific laboratory cultures. The apparent success of the phosphorus inactivation procedure may lead to widespread use, assuming aluminum costs remain moderate, and it would seem important to have data on the possible negative effects of it on lakes and lake organisms.

CONCLUSIONS

The aluminum treatment of lake sediments to control P release and to hasten P-limiting conditions following nutrient diversion appears to be one of our more successful means of improving lake and pond trophic state. Lakes which have received sufficient dose exhibit reduced algal biomass and improved transparency.

Methods of adding aluminum, primarily as aluminum sulfate thus far, have not varied greatly since the design of the Horseshoe Lake, Wisconsin, application system. But dose has varied widely among treatments, and in some cases there was no basis at all for the amount added. This remains a problem. As well, the possibility of long-term toxicity has not been examined, nor do we know of longevity of effectiveness.

This report has briefly summarized the state of our knowledge regarding aluminum treatment of lakes and pools. A larger, more detailed work was developed in 1979-1980 at the Corvallis Environmental Research Laboratory (USEPA) under the direction of Dr. S. A. Peterson (Cooke and Kennedy, 1980, in press). We conclude that this lake and pond restoration procedure can be successful and holds great promise of providing longevity of control of algal biomass. We urge that support be given to those areas which we have designated as important to developing this procedure as a standard lake restoration technique.

ACKNOWLEDGEMENT

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REFERENCES

1. Bandow, F. 1974. Algae control in fish ponds through chemical control of available nutrients. Minn. Dept. Nat. Res., Div. Fish, Wildlife. Invest. Rept. 326. 22 pp.
2. Biesinger, K. E. and G. M. Christensen. 1972. Effects of various metals on survival, growth, reproduction and metabolism of *Daphnia magna*. J. Fish. Res. Bd. Can. 29:1691-1700.
3. Burrows, S. D. 1977. Aquatic aluminum: chemistry, toxicology, and environmental prevalence. CRC Critical Reviews in Environmental Control 7:167-216.
4. Carlson, R. E. 1977. A trophic state index for lakes. Limnol. Oceanogr. 22:361-369.

5. Carlson, R. E. 1979. A review of the philosophy and construction of trophic state indices. In: T. E. Maloney (Ed.), Lake and Reservoir Classification Systems. Ecol. Res. Ser. EPA-600/3-79-074.

6. Cooke, G. D., M. R. McComas, D. W. Waller and R. H. Kennedy. 1977. The occurrence of internal phosphorus loading in two small, eutrophic, glacial lakes in Northeastern Ohio. Hydrobiol. 56:129-135.

7. Cooke, G. D., R. T. Heath, R. H. Kennedy and M. R. McComas. 1978. Effects of diversion and alum application on two eutrophic lakes. EPA-600/3-78-033.

8. Cooke, G. D. and R. H. Kennedy. 1978. Effects of a hypolimnetic application of aluminum sulfate to a eutrophic lake. Verh. Int. Ver. Limnol. 20:486-489.

9. Cooke, G. D. 1979. Evaluation of aluminum sulfate for phosphorus control in eutrophic lakes. OWRT Proj. No. A-053-OHIO. Final Report. Ohio Water Resources Center, Columbus, Ohio.

10. Cooke, G. D. and R. H. Kennedy. 1980. Lake restoration through precipitation or inactivation of phosphorus with aluminum or zirconium salts. Ecol. Res. Ser. in press.

11. Dominie, D. 1978. Cobbossee watershed district lakes restoration project. Progress report #4. Cobbossee Watershed District, Winthrop, Maine.

12. Edmondson, W. T. 1970. Phosphorus, nitrogen, and algae in Lake Washington after diversion of sewage. Science 169:690-691.

13. Eisenreich, S. J., D. E. Armstrong and R. F. Harris. 1977. A chemical investigation of phosphorus removal in lakes by aluminum hydroxide. Tech. Rept. Wisc. Water Resources Center 77-02. Univ. of Wisconsin, Madison, Wisc.

14. Everhart, W. H. and R. A. Freeman. 1973. Effects of chemical variations in aquatic environments. Vol. II. Toxic effects of aqueous aluminum to rainbow trout. EPA-R3-73-011b.

15. Freeman, R. A. 1973. Recovery of Rainbow trout from aluminum poisoning. Trans. Amer. Fish. Soc. 102:152-154.

16. Gasperino, A. F. and R. A. Soltero. 1978. Restoration of Medical Lake: Engineering design and preliminary findings. BN-SA-807. Battelle Northwest, Richland, Washington.

17. Kennedy, R. H. and G. D. Cooke. 1974. Phosphorus inactivation in a eutrophic lake by aluminum sulfate application: A preliminary report of laboratory and field experiments. Conference on Lake Protection and Management, Madison, Wisc.

18. Kennedy, R. H. 1978. Nutrient inactivation with aluminum sulfate as a lake restoration technique. Ph.D. Dissertation, Kent State University. 292 pp.

19. Kennedy, R. H. and G. D. Cooke. 1980. Aluminum sulfate dose determination and application technique. Ecol. Res. Ser. (in prep.).

20. Larsen, D. P., K. W. Malueg, D. W. Schults and R. M. Brice. 1975. Response of Shagawa Lake, Minnesota, USA to point-source phosphorus reduction. Verh. Internat. Ver. Limnol. 19:884-892.

21. May, V. 1974. Suppression of blue-green algal blooms in Braidwood Lagoons with alum. J. Aust. Inst. Agric. Sci. 40:54-57.

22. Moffett, M. 1979. Changes in the microcrustacean communities of East and West Twin Lakes, Ohio, following lake restoration. M.S. Thesis. Kent State University.

23. Narf, R. P. 1978. An evaluation of past aluminum sulfate lake treatments: present sediment aluminum concentrations and benthic insect renewal. Wisc. Dept. Nat. Res., Madison, Wisc.

24. Peterson, J. O., J. J. Wall, T. L. Wirth and S. M. Born. 1973. Eutrophication control: nutrient inactivation by chemical precipitation at Horseshoe Lake, Wisconsin. Tech. Bull. No. 62, Wisc. Dept. of Nat. Res., Madison, Wisc.

25. Peterson, S. A., W. D. Sanville, F. S. Stay and C. F. Powers. 1974. Nutrient inactivation as a lake restoration procedure--laboratory investigations. EPA-660/3-74-032.

26. Sanville, W. D., A. R. Gahler, J. A. Searcy and C. F. Powers. 1976. Studies on lake restoration by phosphorus inactivation. EPA-600/3-76-041.

27. Stumm, W. and J. J. Morgan. 1970. Aquatic Chemistry. An Introduction Emphasizing Chemical Equilibria in Natural Waters. Wiley-Interscience. New York. XV + 583 pp.

AERATION/CIRCULATION FOR CONTROL OF ALGAL PRODUCTION

Robert A. Pastorok
Thomas C. Ginn
Marc W. Lorenzen

Tetra Tech, Inc.
1900 116th Avenue, N.E.
Bellevue, Washington 98004

INTRODUCTION

Artificial aeration or circulation of lakes is commmonly used for managing the ecological consequences of eutrophication. Unlike techniques that prevent nutrient influx from the watershed, aeration/circulation affects nutrient cycling within the lake only. It can be used to improve water quality by alleviating a variety of problems which arise during thermal stratification and deoxygenation of the hypolimnion. Aeration/circulation has proved beneficial in management of domestic water supplies, downstream releases from reservoirs, and industrial water systems. By inducing dramatic changes in biological communities through influences on species abundance and distribution, diversity, and trophic structure, the technique has potential usefulness in control of algal blooms and improvement of fisheries. In some instances, treatment has aggravated already existing problems or caused new problems to arise, but these results can usually be attributed to faulty design of the aeration device, improper application of the technique, or inadequate understanding of the biological community and its response mechanisms.

The broad range of aeration/circulation techniques has been divided into two major groups: artificial circulation and hypolimnetic aeration. Procedures which are designed to either mix the whole lake or provide aeration without maintaining the normal thermal structure are classified as artificial circulation techniques. Within this category, systems range from high-energy mixing devices to low-energy aeration procedures; mechanical pumps, rising air bubbles and jets of water can serve as mixing devices. In most cases, mixing has been induced after the development of normal thermal stratification; hence it is often termed artificial destratification. Destratification restores oxygen to deficient hypolimnetic waters, whereas artificial circulation before the onset of stratification can maintain aerobic conditions throughout a lake. Either technique leads to habitat expansion for zooplankton, benthos and warm-water fish. However, complete mixing may eliminate the cold-water habitat at mid-water or near the lake bottom and cold-water fishes such as the salmonids may disappear from the lake. Under certain circumstances, artificial circulation can eliminate excessive algal growth or shift the community away from a uni-specific bloom of a blue-green alga toward a mixed assemblage of more desirable green algae.

Hypolimnetic aeration allows oxygenation of the bottom waters of a lake without disrupting the normal pattern of thermal stratification. Both air and oxygen in compressed form have been used. Hypolimnetic aeration can effectively maintain aerobic conditions without loss of the cool hypolimnetic water preferred for domestic and industrial uses and required for the maintenance of cold-water fisheries.

This paper is limited to a review of artificial circulation and does not consider hypolimnion aeration further. The effects of circulation on zooplankton and fishes is also beyond the scope of this paper.

MIXING DEVICES AND APPLICATIONS

The techniques used to circulate lakes can be broadly classified as diffused air systems or mechanical mixing systems. The former category includes all aeration devices exploiting the "air-lift" principle; i.e. water is upwelled by a plume of rising air bubbles. Mechanical systems employ standard pumps, fan blades, or water jets to move water. After reviewing design and field performance of a variety of destratification techniques, Lorenzen and Fast (1977) concluded that diffused air systems are less expensive and easier to operate than mechanical mixing devices.

Compressed air is usually injected into the lake through a perforated pipe or other simple diffuser (e.g. Fast 1968; Haynes 1973). Release of air in deep water forms a trail of rising air bubbles which entrain water all along their paths, creating turbulent mixing around a central zone of upwelling (Kobus 1968; see figure A-1 in Lorenzen and Fast 1977). Kobus (1968) has shown that the amount of water flow induced by a rising bubble plume is primarily a function of air release depth and air flow rate. Therefore, artificial circulation is generally most effective if air is injected at the maximum depth possible (Fast 1968). Lorenzen and Fast (1977) conclude that about 9.2 m^3/min of air per 10^6 m^2 of lake surface (= 30 SCFM per 10^6 ft^2) will provide adequate water movement for surface aeration, with minimal variations in temperature ($< 2^{\circ}C$) and algal concentrations throughout the water column. According to this scaling rule, most aeration systems used in the past have been undersized (Table 1).

Although most air compressors have been driven by electricity or gasoline combustion, alternative energy sources are possible. For example, Rieder (1977) has successfully coupled a wind power generating system with an air compressor capable of destratifying small prairie lakes.

Mechanical mixing devices have been used less frequently than diffused air systems, although they may be quite successful in certain circumstances (e.g. Irwin et al. 1966; Toetz 1977a, b; Garton et al. 1978). A pumping rate of about 10.9 m^3/min was sufficient to destratify Stewart Hollow Reservoir and Vesuvius Reservoir within 8 days (Table 1; Irwin et al. 1966). However a pumping capacity of about 1.3 m^3/min over a period of 10.1 days did not give a complete mix of West Lost Lake (Hooper et al. 1953).

The axial flow pump designed by Quintero and Garton (1973) (also see Garton and Punnett 1978; and Garton et al. 1978) uses a large fan blade to move water from the lake surface downward. A pump with a capacity of 102 m^3/min completely destratified Ham's Lake after 3 days of operation in 1975 (Toetz 1977b). On the other hand, an array of 16 pumps with a total capacity of 1,600 m^3/min failed to mix Arbuckle Lake completely, although it did lower the thermocline (Toetz 1979). Arbuckle Lake is more than twice as deep as Ham's Lake (Table 1).

The Metropolitan Water Board of London induces mixing in water supply reservoirs by discharging relatively warm river water from jet-type inlets located near the bottom of each impoundment. A series of 9 jets, each with a capacity of about 108 m^3/min achieved adequate circulation in Queen Elizabeth II Reservoir (Ridley et al. 1966).

EFFECTS OF ARTIFICIAL CIRCULATION ON WATER QUALITY

The onset of anaerobic conditions in the hypolimnion of a stratified lake causes extensive chemical transformations in the surficial sediments, which result in a transfer of nutrients to the overlying water (Mortimer 1941, 1942; Hutchinson 1957). The subsequent accumulation of Fe, CO_2, H_2S, NH_4^+ and other chemicals in the hypolimnion creates problems of quality control for utilities supplying domestic and industrial waters (e.g. Teerink and Martin 1969). Oxygenation of hypolimnetic waters raises the redox potential near the lake bottom, greatly lowering concentrations of reduced chemical species and eliminating taste and odor problems. Most aeration systems have been installed with this goal in mind (Smith et al. 1975; Fast 1979a).

In a survey of 26 water suppliers conducted by the American Water Works Association, 86 percent of the utility managers considered their artificial destratification projects a success (AWWA 1971). However, 46 percent reported that mixing created new water quality problems. Most of the problems created by treatment involved elevation of turbidity levels or algal blooms.

CHEMICAL PARAMETERS

In most cases, artificial destratification increases the concentration of dissolved oxygen in bottom waters immediately (e.g. Hooper et al. 1953; Lackey 1972; Haynes 1973); dissolved oxygen in the former epilimnion may show a corresponding decrease due to a reduction in photosynthesis (Haynes 1973) or mixing of hypolimnetic waters with low dissolved oxygen and high BOD into the surface layer (Ridley et al. 1966; Thomas 1966). Over a period of several weeks, the oxygen content of the whole lake is increased (Table 1). The method of destratification is probably irrelevant to the rate of oxygenation as long as an adequate mix can be maintained. Since the direct transfer of oxygen between rising air bubbles and water is unimportant except in very deep lakes, the primary mode of aeration is through atmospheric exchange at the lake's surface, even with diffused air systems (King 1970; Smith et al. 1975).

TABLE 1. SELECTED LAKES AND THEIR PHYSIC

Lake	Location	Reference	Depth (m)			Volume x 10^{-6} (m^3)
			Max.	Mean	Air	
Cline's Pond	Oregon	Malueg et al. 1971	4.9	2.5	4.9	0.003
Parvin Lake	Colorado	Lackey 1972	10	4.4	10	0.849
Section 4 Lake	Michigan	Fast 1971a	19.1	9.8	18.3	0.110
Boltz Lake 1966	Kentucky	Symons et al. 1967, 1970 Robinson et al. 1969	18.9	9.4	18.9	3.614
University Lake	North Carolina	Weiss and Breedlove 1973	9.1	3.2	9.1	2.591
Kezar Lake	New Hampshire	N.H.W.S.P.C.C. 1971 Haynes 1973	8.2	2.8	8.2	2.008
King George VI 1965 1966	United Kingdom	Ridley et al. 1966	16			
Indian Brook Res.	New York	Riddick 1957	8.4		2.2	
Prompton Lake	Pennsylvania	McCullough 1974	10.7		10.7	4.193
Cox Hollow 1966 1967-69	Wisconsin	Wirth and Dunst 1967 Wirth et al. 1970	8.8	3.8	8.8	1.480
Stewart Lake 1974 1975	Ohio	Barnes and Griswold 1975	7			
Wahnbach Res. 1961-62 1964	W. Germany	Bernhardt 1967	43	19.2		41.618
Starodworskie Lake	Poland	Lossow et al. 1975	23		23	
Queen Elizabetn II Res. 1965 1966	United Kingdom	Ridley et al. 1966	17.5		17.5	
Lake Roberts	New Mexico	R. S. Kerr Res.Center 1970 McNail 1971	9.1		9.1	1.233
Falmouth Lake	Kentucky	Symons et al. 1967, 1970 Robinson et al. 1969	12.8	6.1	12.8	5.674
Test Res. II	United Kingdom	Knoppert et al. 1970	10.7	9.4	10.7	2.405
Ham's Lake 1973 1975	Oklahoma	Steichen et al. 1974 Toetz 1977a, b Garton et al. 1978	10	2.9	1.2	115
Test Res. I	United Kingdom	Knoppert et al. 1970	10.7	9.4	10.7	2.097
Mirror Lake 1972 1973	Wisconsin	Smith et al. 1975 Brynildson and Serns 1977	13.1	7.6	12.8	0.340
Stewart Hollow Res.	Ohio	Irwin et al 1966	7.6	4.6	pump 7.6	0.148
Cladwell Res.	Ohio	Irwin et al. 1966	6.1	3.0	pump 6.1	0.123
Pine Res.	Ohio	Irwin et al. 1966	5.2	2.1	pump 5.2	0.121

/

YSICAL-CHEMICAL RESPONSES TO ARTIFICIAL CIRCULATION

	Area (ha)	Aeration Intensity[a] Q_A (m^3/min)	Aeration Intensity[a] Q_A/V x 10^6	Aeration Intensity[a] Q_A/A x 10^6	ΔT[b] (°C) Before	ΔT[b] (°C) After	Lake Response[c] SD	DO	PO_4	TP	NO_3	NH_4	Fe Mn
33	0.4	0.028	10.2	7.08	6	0	+	+	+		0	0	
49	19	2.1	2.5	11.18	6	<3		+			0		-
10	1.1	2.21	20	200	15	0	-	+					
14	39	3.17	0.88	8.17	9-10	<2	-	-		-	+	+ -	-
01	80.9	0.40	0.15	0.49		<2	-	+ 0	-	-	+	-	-
08	73	2.83	1.41	3.88	11	<1	+	+	+	+	+ -	-	-
	142		water jet		6.5 6.5	6 4		+ +					
	7.3	4.53		62.06	9	0		+					-
93		4.53	1.08			1							
00	38.8	2.04	1.38	5.26	17	<3	+ 0	+ +	- -		+	- -	- -
	2.4				19 18	5 7		+ +	0 0		- -		
18	214	2.01 5.95	0.048 0.143	0.94 2.78	14	6		+ 0 +					- -
	7	0.27		3.81	15	<2		+	-	-	+	-	
	128		water jet		6 4	0 0		+ -	+				
33	28.3	3.54 2.26	2.87 1.84	12.51 8.00	6 4.6	0 0		+ -		- +			
74	91	3.26	0.58	3.58			-	±		-	0	-	-
05	25.4	2.01	0.84	7.92		0	-	+		0	-	-	
	40		axial-flow pump		13.5 10	<1 <2	+	+ +	+		-	-	-
97	22.7	2.01	0.96	8.86		0	0	+		0	-	-	
40	5.3	0.45	1.13	8.55	13	0 0		+ +	- 0	+ -			
08	3.3		axial-flow pump		22 15	13 <2		0 0					
33	4.0		axial-flow pump		20	7		+					
21	5.7		axial-flow pump		13	3		-					

2

TABLE 1. (continued)

Lake	Location	Reference	Depth (m)			Volume x 10^{-6} (m^3)	Ar (h
			Max	Mean	Air		
Vesuvius Res.	Ohio	Irwin et al. 1966	9.1	3.6	pump 9.1	1.554	62.
Vaxjosjon	Sweden	Bengtsson and Gelin 1975	6.5	3.5	6	3.1	97
Corbett Lake	British Columbia	Halsey 1968 Halsey and Galbraith 1971	19.5	7	19.5	1.689	24.
Buchanan Lake	Ontario	Brown et al. 1971	13	4.9	13	0.42	8.
Lake Maarsseveen	United Kingdom	Knoppert et al. 1970	29.9	14	19 29.9	8.018	60.
Arbuckle Lake 1975 1977	Oklahoma	Toets 1977a, b; 1979	24.7	9.5	6 pump 2 pump	8930	951
Casitas Res.	California	Barnett 1975	82	26.8	39- 55	308	1100
Hyrum Res.	Utah	Drury et al. 1975	23	11.9	15.2	23.1	190
West Lost Lake	Michigan	Hooper et al. 1953	12.8	6.2	pump 11.9	0.089	1.
Waco Res.	Texas	Biederman and Fulton 1971	23	10.7	23	128	2942
Lake Catherine	Illinois	Kothandaraman et al. 1973	11.8	5	8.5	3.034	19.
El Capitan 1965 1966	California	Fast 1968	62	9.8 9.4	21.3 28.3	17.99 21.05	113. 222
Lake Calhoun	Minnesota	Shapiro and Pfannkuch 1979	27.4	10.6	23	18.01	170.
Eufaula Res.	Oklahoma	Leach et al. 1970	27	16.2	27	703.1	41480
Pfaffikersee	Switzerland	Thomas 1966 Ambuhl 1967	35	18	28	56.5	325

[a] Q_A = rate of air injection (m^3/min), V = volume (m^3), A = area (m^2)

[b] ΔT = temperature differential between surface and bottom water

[c] Response parameters: SD = secchi depth, DC = dissolved O_2, PO_4 = phosphate,

TP = total phosphorus, NO_3 = nitrate, NH_4 = ammonium,

Fe = iron, Mn = manganese

Direction of change in average concentration for whole lake: + = increase, - = decrease, 0 = no significant change.

[d] Mixed to air release depth

		Aeration Intensity[a]								Lake Response[c]		
Area (ha)	Q_A (m^3/min)	Q_A/V $\times 10^6$	Q_A/A $\times 10^6$	ΔT^b (°C) Before	After	S D	D O	PO_4	T P	NO_3	NH_4	Fe Mn
42.5		axial-flow pump		16	2		0					
87	7.2	2.32	8.28		0		+		+			
24.2	4.50	2.66	18.52	2-4	0		+					
8.9	0.28	0.67	3.17		0	-	+		-		-	-
60.7	2.49	0.31	4.10	8	0							
951		axial-flow pump		11 9	9 13	0 0	0 +	0 +		0 +	0 -	0
1100	17.84	0.06	1.62		d	+ 0						-
190	2.83	0.17	1.49	6	2-4	-	+	0	0	-	-	
1.4	pump			13	9	-	+		+			
2942	3.11	0.02	0.10	17	~6		+					
59.5	0.76	0.25	1.27	2	0-14	0	+	0	0	0	0	0
183.9	6.09	0.34	3.31	~9	<3	-	+					-
222	6.09	0.29	2.74	~6	<3	-	+					-
170.4	2.83- 3.54	0.16- 0.20	1.66- 2.08	16	9^d	-	+					
41480	33.98	0.05	0.06	10	7		0					
325	6	0.11	1.85				+			+	-	

change.

Under some circumstances, oxygen depletion cannot be prevented by normal levels of artificial aeration (Table 1). For example, during mixing of Lake Roberts in July, a combination of reduced phytosynthetic activity in cloudy weather and an unusually high BOD caused by decomposing Anabaena scums created anoxic conditions throughout the lake leading to a massive fish-kill (R.S. Kerr Research Center 1970; McNall 1971).

Oxygen levels influence redox reactions involving Fe, Mn and Al; in turn, these elements and their complexes partly determine the availability of nitrogen and phosphorus compounds through release processes occurring at the surface of profundal sediments (Mortimer 1941, 1942; Hutchinson 1957). Because of the importance of nutrient regeneration to algal production and the interaction of chemical and biological components in controlling nutrient levels, the effects of artificial circulation on phosphorus and nitrogen concentrations is discussed below in the section on plankton.

As hypolimnetic waters are brought to the lake's surface, excess gases such as CO_2, H_2S, and NH_3 are released to the atmosphere (R.S. Kerr Research Center 1970; Toetz et al. 1972; Haynes 1973). Along with oxygen and other chemical species, these gases become isochemical with depth (Toetz et al. 1972). Temporary rises of H_2S and NH_3 may occur in surface waters following mixing (R.S. Kerr Research Center 1970). Undoubtedly, nitrification of NH_4^+ to NO_3^- is an important mechanism for elimination of reduced ammonia compounds (Brezonik et al. 1969). After mixing, the concentration of CO_2 in the surface layer rises as hypolimnetic levels decrease. The CO_2 content of the entire lake often falls slightly (Riddick 1957; Haynes 1973; Steichen et al. 1974), although temporary increases are sometimes observed; e.g. during the 1966 mixing of Boltz Lake (Robinson et al. 1969). Since changes in ambient CO_2 levels and related pH effects have an important influence on species interactions in the phytoplankton community, these topics will be discussed in detail in a later section.

Some air injection systems may cause supersaturation of nitrogen gas (N_2) relative to surface hydrostatic pressures (Fast 1979a, b). Dissolved nitrogen concentrations of only 115 to 120 percent saturation can induce substantial mortality among salmonids in rivers (Rucker 1972) and in laboratory experiments (Blahm et al. 1976). Normally, the entire water column is close to 100 percent saturation with respect to depth-specific temperatures and pressures (Hutchinson 1957). Any rise in N_2 above the ambient concentrations is a potential problem when reservoir waters are released downstream.

Fast (1979a, b) discusses the problem of N_2 supersaturation during artificial destratification of Casitas Reservoir in 1977. After 80 days of aeration at 46 m depth, N_2 levels in the zone of induced mixing (15 to 45 m) were at 125 percent saturation relative to surface pressures. The waters below 46 m had even higher N_2 concentrations, up to 140 percent saturation relative to the surface.

Presumably, the aeration system did not greatly influence N_2 levels below the depth of air release, so such high concentrations may be normal for this reservoir.

During spring circulation, N_2 levels throughout the lake generally equilibrate at 100 percent saturation with respect to surface temperature and pressure. Any warming of the hypolimnion during summer will result in supersaturation relative to surface pressure and ambient temperature at depth. But hydrostatic pressure probably maintains this "excess" gas in solution throughout the metalimnion and hypolimnion. Even after hypolimnetic aeration of Lake Waccabuc, N_2 levels for most of the water column were below the 100 percent saturation values adjusted for both temperature and pressure (Fast et al. 1975a).

In any event, absolute concentrations of N_2 will increase with depth in stratified lakes, and the lower waters will be supersaturated relative to the surface (Hutchinson 1957; Fast 1979a). If the body fluids of fish equilibrate at N_2 levels in deep water, and then the fish migrate to near the surface, gas bubbles could form causing stress or mortality. To what extent this occurs naturally, and whether aeration aggravates the problem remains unknown. In Casitas Reservoir, fish-kills were avoided because surface waters remained close to saturation and bottom waters were not released downstream (Fast 1979b).

PHYSICAL PARAMETERS

In almost every case, artificial circulation during summer promotes an increase in the heat content of the lake, even when mixing is incomplete (e.g. Toetz et al. 1972; Haynes 1973; Toetz 1977b, 1979; Kothandaraman et al. 1979). Usually, the temperature of the upper waters decreases by a few degrees, whereas deep waters are warmed by as much as 15 to 20 °C to approximately the same temperature as the surface. Circulation during winter actually reduces water temperatures overall because bottom waters are no longer insulated from the cooler air by a surface layer of water or ice (Lackey 1972; Drury et al. 1975).

Isothermy is difficult to establish because the destratification process becomes less efficient as the lake comes closer to a complete mix (Fast 1979a). Unfortunately, most destratification devices are low energy systems, and a majority have been undersized with respect to the scaling rule suggested above (Table 1; Lorenzen and Fast 1977). When more thermal energy is absorbed at the lake's surface than the circulation device can distribute, then microthermal stratification of 2 to 3°C provides algal populations a surface refuge with high light levels (e.g. Fast 1973a; Drury et al. 1975).

In small lakes, horizontal mixing is relatively complete, but in large reservoirs, the destratification system will influence a limited area (e.g. Leach et al. 1970; McCullough 1974). Of course, unaffected sections of the lake may provide excellent experimental controls.

Artificial circulation has varied effects on water transparency, depending on the intensity of mixing and the contribution of phytoplankton to turbidity levels before treatment. In four of the lake case histories examined, artificial mixing resulted in greater water transparency; and in 13 cases, transparency decreased or stayed the same (Table 1). When mixing is induced during a surface bloom of blue-green algae, transparency will increase immediately due to distribution of the algae throughout a greater water volume (Haynes 1973). Thereafter, water clarity may be enhanced by destruction of the bloom through light limitation in deep lakes (Lorenzen and Mitchell 1975) or through a change in some other environmental factor in shallow lakes (Malueg et al. 1971). In contrast water clarity was reduced in Section Four Lake when intense aeration resuspended inorganic sediments and detritus from the lake bottom, nullifying the effect of a slight decline in phytoplankton (Fast 1971a). A rise in total seston after mixing generally correlates with a decrease in transparency (Fast 1971a; Drury et al. 1975; Garton 1978; Garton et al. 1978). In West Lost Lake and Hyrum Reservoir, algal blooms were responsible for the observed changes (Hooper et al. 1953; Drury et al. 1975).

EFFECTS OF ARTIFICIAL CIRCULATION ON PHYTOPLANKTON

The effects of artificial circulation on phytoplankton populations are extremely variable (see Toetz et al. 1972 for an earlier review), not only because application of techniques and efficiency of mixing devices vary among investigations, but also because alternative biological communities exhibit different responses to the same kinds of perturbations. Moreover, the desirability of a particular response depends on management goals. For example, an increase in planktonic algae will be considered a nuisance if it causes filter clogging and "taste and odor" problems in a water supply system (Teerink and Martin 1969) yet the same "bloom" could have beneficial effect by stimulating fish production (e.g. Johnson 1966; Oglesby 1977). An understanding of the mechanisms underlying responses of specific biological systems is essential to enhancement of our predictive power in future applications of circulation techniques.

At one time, artificial circulation was regarded as a method for reducing algal growth by one or more of the following mechanisms (Fast 1975):

1. "Preventing nutrient regeneration during anaerobic conditions and thereby reducing internal loading
2. Increasing the mixed depth of the algae and thereby reducing algal growth due to light limitation

3. Subjecting the algae to turbulence and rapid changes in hydrostatic pressure as they are swept through a large vertical distance of the water column."

It is now obvious that other effects of artificial circulation may negate these influences and in some instances produce an opposite result, i.e. increased algal biomass. In fact, of the 40 experiments in which destratification was relatively complete, only 65 percent (=26 experiments) led to any significant change in algal concentrations; of these, about 30 percent resulted in more algae than before destratification. Table 2 summarizes the responses of phytoplankton to artificial circulation for each lake. When more than one experiment was conducted in a lake, the predominant response is given unless the data are too variable to indicate an overall trend; then, the responses for individual experiments are given. Where mixing was complete, aeration caused a decrease in algal density or biomass in 13 of 23 lakes. In three lakes, the amount of phytoplankton remained about the same, and in seven lakes it increased or the overall response was unclear. Where mixing was incomplete, algal density generally stayed the same or increased following treatment (Table 2). Although artificial circulation usually has a negative influence on blue-green algae, its effect on green algae is ambiguous.

Changes in phytoplankton populations after circulation treatment are discussed below under three primary modes of influence: physical, chemical, and biological mechanisms.

PHYSICAL MECHANISMS

In lakes where algal production is potentially limited by light, several models predict a decrease in net photosynthesis and a reduction in standing crop of algae as depth of the mixed layer increases (Murphy 1962; Lorenzen and Mitchell 1975; Oskam 1978). Since destratification effectively increases the depth of mixing, algae will then be spending a considerable amount of time in dimly lit zones, perhaps below the compensation level in deep lakes. Accordingly, Haynes (1973) observed a sharp decline in primary production soon after aeration of Kezar Lake (although values thereafter rose gradually to predestratification levels). At Lake Vaxjosjon (Sweden), average primary production ($gC/m^2 \times d$) during summer of 1970 decreased by about 30-40 percent relative to the control year(Bengtsson and Gelin 1975). When aerators were operative for only two brief periods in summer 1971, average production was only slightly lower than pretreatment levels. Toetz (1979) found that even partial mixing of Arbuckle Lake caused a large drop in net primary production and a small but significant reduction in the ratio gross production:community respiration.

Lorenzen and Mitchell (1975) have found good agreement between the predictions of their model, relating maximum standing crop of algae to mixed depth, and the results of experiments at Kezar Lake,

TABLE 2. RESPONSES OF PHYTOPLANKTON TO ARTIFICIAL CIRCULATION[a]

Lake	Reference	Algal Density[c]	Algal Standing Biomass[d]	Mean Chlorophyll-a Concentration	Green Algae	Blue-green Algae	Ratio Gr : Bl-gr
Complete Mixing							
Cline's Pond	Malueg et al. 1971	-		-	0	-	+
Parvin Lake	Lackey 1973a	-			-	0[e]	0
Section 4 Lake	Fast 1971a Fast et al. 1973	-[f]	-		-		
Boltz Lake	Symons et al. 1967, 1970 Robinson et al. 1969	-	-		-	-	+
University Lake	Weiss and Breedlove 1973	-		0	+	-	+
Kezar Lake	Turner et al. 1972 Haynes 1973 N.H.W.S.P.C.C.1971 Lorenzen and Mitchell 1975	-	-	0	+	-	+
King George VI	Ridley et al. 1966	-			-	+	-
Indian Brook[b]	Riddick 1957	-					
Prompton Lake[b]	McCullough 1974	-					
Cox Hollow[b]	Wirth and Dunst 1967 Wirth et al. 1970	-					
Stewart Lake	Barnes and Griswold 1975			-			
U.K. Reservoir[b]	Ridley 1970					-	
Wahnbach Reservoir	Bernhardt 1967					-	
Queen Elizabeth II		$\underset{-}{0}$					
Lake Roberts	McNall 1971 R.S. Kerr Res. Cen. 1970	±				±	
Falmouth Lake	Symons et al. 1967, 1970 Robinson et al. 1969	+			+	-	+
Test Res. II	Knoppert et al. 1970	+	+		0	+	0
Buchanan Lake	Brown et al. 1971	+	+	+	+	-	+
Ham's Lake[f]	Steichen et al. 1974 Toetz 1977a, b Garton 1978	0		0	0	0	0
Test Res. I	Knoppert et al. 1970	0+	0+			0+	0-

TABLE 2. (continued)

Lake	Reference	Algal Density[c]	Algal Standing Biomass[d]	Mean Chlorophyll-a Concentration	Green Algae	Blue-green Algae	Ratio Gr : Bl-gr
Mirror Lake	Smith et al. 1975 Knauer 1975	0[g]	0[g]			0[g]	
4 Lakes[h]	Irwin et al. 1966	0				-	+?
Starodworskie Lake[f]	Lossow et al. 1975				-	+	-
Incomplete Mixing							
Casitas Res.[b]	Barnett 1975	-				-	
Hyrum Res.	Drury et al. 1975	+	+	+	-	+	-
West Lost Lake	Hooper et al. 1953	+	+			+	
Pfaffikersee	Thomas 1966	+				+	
Waco Res.[b]	Biederman and Fulton 1971	0			0		
Lake Maarsseveen[b]	Knoppert et al. 1970	0			0		
Lake Catharine	Kothandaraman et al. 1979	0					0
El Capitan[f]	Fast 1973	+?					0
Arbuckle Lake	Toetz 1977a, 1979	0		0			0
Lake Calhoun	Shapiro and Pfannkuch 1973		+	+	0	+	-

[a] + = increase, - = decrease, 0 = no significant change

[b] qualitative information only

[c] cells or colonies per liter; weighted mean for water column unless noted

[d] weight per square meter of lake surface

[e] increase observed, but control year was unusual

[f] samples were taken near lake surface

[g] increase observed, but it was correlated with large input of allochthonous nutrients

[h] Stewart Hollow Lake, Caldwell Lake, Pine Lake, Vesuvius Lake

New Hampshire (Figure 1). Although the model ignores the effects of mixing on algal losses by sinking, grazing, and parasitism, it does appear to give a reasonable estimate of maximum standing stock in a variety of circumstances. Perhaps more importantly, it explains the apparently conflicting results obtained by different studies of changes in algal abundance after mixing (Table 2). If algae are limited by nutrients before circulation, a slight increase in mixing depth could cause an elevation of standing crop (e.g. point A to point B in Figure 1), a result opposite to that found in the light limited condition. Thus primary productivity and productivity per cell during aeration of oligotrophic Section Four Lake were up to three times higher than values during the control year (Fast 1971a). The particularly intense aeration/circulation of this lake (Table 1) resuspended large quantities of bottom detritus and probably made nutrients more available to algae. If mixing shifts the controlling mechanism from nutrient limitation to light limitation, a moderate increase in mixed depth will cause a substantial rise of peak algal biomass or at best only a slight decline (A to C or B to C respectively in Figure 1). However, for large increases in mixed depth the imposition of light limitation can cause substantial decreases in water column algal biomass (A and B to D in Figure 1). It should be noted that when water column biomass decreases with increased mixed depth the concentration of algae will decrease dramatically because less biomass is distributed in a much larger water volume. Finally, because of differences in growth parameters among algal species, a major shift in species composition of phytoplankton could generate a change in peak quantity of algae apart from the effects of mixed depth.

Where algal abundance is relatively low, e.g. in oligotrophic lakes, artificial destratification usually produces little change in cell concentrations (Knoppert et al. 1970; Biederman and Fulton 1971; Toetz 1977a, b; but see Fast 1971a). In some instances, standing stock may have increased due to change in mixing depth, whereas in others, the change was small as a result of incomplete destratification. In any event, since the slope of the ascending curve in Figure 1 equals the peak nutrient-limited concentration of algae (Lorenzen and Mitchell 1975), the slope will be smallest for oligotrophic lakes because these yield less algae per unit volume than do entrophic lakes. Hence, any given change in mixed depth over the range of nutrient-limited biomasses will result in only small displacements of standing crop in oligotrophic lakes compared with potential shifts in richer lakes.

A critical problem arises when surface waters heat rapidly and an undersized circulation device is unable to achieve a complete mix (i.e. isothermy). The resulting microstratification provides a shallow-water "refuge" for some blue-green algae (e.g. Aphanizomenon flos-aquae), yielding greater population densities after the aeration treatment (e.g. Thomas 1966; Drury et al. 1975). The influence on standing crop is unpredictable, depending upon the magnitude of the actual decrease in mixed depth and the mode of limitation (cf. Figure

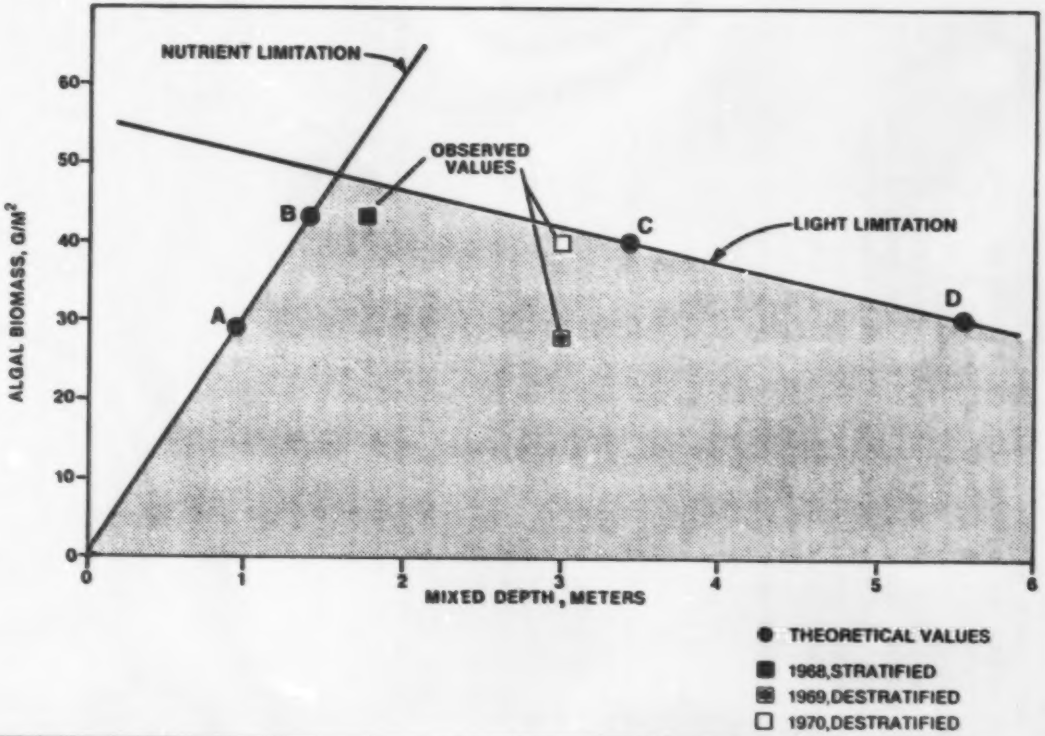


FIGURE 1
THEORETICAL AND OBSERVED PEAK BIOMASS OF ALGAE
IN KEZAR LAKE (ADAPTED FROM LORENZEN AND MITCHELL 1975)

1). In El Capitan Reservoir, incomplete mixing resulted in microstratification near the lake surface and an increase in net primary productivity over pretreatment levels (Fast 1973a). The use of a mechanical device like the Garton pump (Quintero and Garton 1973; Garton and Punnett 1978; Garton et al. 1978), which induces mixing by moving surface waters downward, might prevent microstratification and associated problems.

When circulation treatment is effective, the increased depth of mixing does lead to an expansion of the depth distribution of phytoplankton (Fast 1971a; Haynes 1973). Apart from long-term effects on standing crop, if a roughly uniform profile of cell concentration versus depth is obtained soon after mixing, population densities decline and water clarity is enhanced (e.g. N.H.W.S.P.C.C. 1971; Haynes 1973).

On the other hand, artificial circulation sometimes reduces light penetration by creating more turbid waters through resuspension of bottom deposits (Hooper et al. 1953; Fast 1971a). Water-jet inlet systems such as the one used at Queen Elizabeth II Reservoir (United Kingdom)(Ridley et al. 1966) especially aggravate this problem by reducing sedimentation of debris.

The high turbulence also helps to retain algal cells in suspension, reducing population losses due to sinking in otherwise susceptible forms like *Asterionella formosa* (Bernhardt 1967; Fast et al. 1973; cf. Lehman and Sandgren 1978) and especially *Microcystis* spp. (Knoppert et al. 1970; Weiss and Breedlove 1973).

Artificial circulation effectively reduced the abundance of blue-green algae in only 19 of the 30 experiments in which mixing was complete; however, these 19 cases represent 76 percent of the instances where any change was noted. Blue-green species often control their depth distribution via buoyancy regulation to take advantage of specific optima in light, temperature and/or nutrients (Fogg and Walsby 1971; Konopka et al. 1978). Following artificial circulation, Bernhardt (1967) and Weiss and Breedlove (1973) observed dispersion of metalimnetic populations and overall decline of *Oscillatoria rubescens* and *O. tenuis* respectively. Whatever the mechanism, *Anabaena* spp. are among the most sensitive forms (Ridley 1970; Knoppert et al. 1970; Malueg et al. 1971; Steichen et al. 1974; Barnett 1975).

CHEMICAL MECHANISMS

Occasionally, researchers interested in elevating fish yield have successfully stimulated phytoplankton growth by mixing nutrient-rich bottom waters into the trophogenic zone, which is generally poorer in dissolved inorganics required by algae (Hooper et al. 1953; Hasler 1957; Schmitz and Hasler 1958). In this case, an incomplete mix is desirable for deep lakes where the maximum depth is greater than the mixed depth necessary to achieve significant light limitation (cf. Figure 1). Johnson (1966) reported an increase in production of phytoplankton and fishes after incomplete destratification of Erdmann Lake; unfortunately, his experimental design was confounded by application of rotenone before mixing.

Mixing techniques have been applied in attempts to reduce algal blooms by curtailing regeneration of nutrients from profundal sediments (Toetz et al. 1972; Dunst et al. 1974; Fast 1979a). Direct aeration of bottom waters combined with increased exchange across the air-water interface leads to reoxygenation of the hypolimnion. Only five studies reported a decrease in whole lake O_2 following artificial circulation (Table 1); in these cases, resuspension of bottom detritus probably increased BOD beyond the neutralization capacity of the oxygenation technique. If the hypolimnion was previously anoxic, oxygenation will immediately reduce average $PO_4^{\equiv}$ concentration in the deep water and in the lake as a whole by precipitation of Fe^{+++} and Mn^{++} complexes (Fitzgerald 1970; Wirth et al. 1970; Haynes 1973; Weiss and Breedlove 1973; Toetz 1979), although $PO_4^{\equiv}$ may occasionally increase in the upper waters (R.S. Kerr Research Center 1970; Toetz 1979). When aeration is insufficient, e.g. during destratification of Queen Elizabeth II Reservoir by water jets, mixing may result in uniform $PO_4^{\equiv}$ levels throughout the water column without causing a decrease in the lower waters (Ridley et al. 1966).

An effective circulation will immediately reduce concentrations of NH_4^+ in the hypolimnion and throughout the lake, mainly by nitrification of NH_4^+ to NO_3^-, as the latter shows a corresponding rise (Brezonik et al. 1969; Weiss and Breedlove 1973; Toetz 1979).

Formation of an oxidized microzone at the sediment-water interface raises the redox potential of surficial mud and forms a barrier to the release of dissolved phosphate ions from the decomposing sediments (Mortimer 1941, 1942); hence the term "bottom-sealing" has sometimes been applied to circulation techniques (Shapiro 1979). Some recent work (Porcella et al. 1970; Kamp-Nielsen 1974, 1975) indicates that some phosphorus still moves across the interface into the well-oxygenated water, but aerobic muds might still act as a net "sink" for phosphorus (Mortimer 1971; Graetz et al. 1973).

Fast (1971a, 1975, 1979a) questions whether artificial circulation reduces internal loading of phosphorus as has previously been assumed. Although $PO_4^{\equiv}$ concentrations are indeed lowered by destratification, the flux of nutrients from profundal sediments to the overlying water and subsequent uptake by the plant community could actually increase. Under aerobic conditions, the higher temperatures in the sediments after destratification will stimulate decomposition and release of phosphorus to overlying waters (Hargrave 1969, Kamp-Nielsen 1975). Simultaneously, nutrient exchange across the mud-water interface is facilitated by increased flow of water over the sediments and invasion of burrowing macroorganisms which mix the sediments vertically (see below). Although tubificid worms are unimportant in stimulating phosphorus release from sediments (Davis et al. 1975; Gallepp et al. 1978), chironomid larvae do facilitate phosphorus transfer from mud to water, possibly in a density-dependent manner (Porcella et al. 1970; Gallepp et al. 1978). Lastly, it is unlikely that circulation techniques can reduce internal loading of nutrients from sources other than the profundal sediments; e.g. "leakage" from littoral macrophytes (Demarte and Hartman 1974; Lehman and Sandgren 1978).

Even if artificial circulation does reduce phosphorus regeneration from the sediments, significant changes in the biota will occur only if 1) internal loading of nutrients is large relative to input from the watershed and 2) algal growth is limited by phosphorus (Fast 1975). Although the latter appears true in many instances (Likens 1972), Lane and Levins (1977) caution against overreliance on the concept of a single limiting nutrient. Also, lakes with nuisance algal blooms are usually eutrophic and, by definition, experience high external loading. In Mirror Lake, Wisconsin, blooms of Oscillatoria noted by Smith et al. (1975) during the fall 1972 and spring 1973 mixing experiments were probably caused by allochthonous inputs of phosphorus via storm sewers rather than by some direct effect of circulation (Knauer 1975).

The effects of destratification on the concentrations of dissolved inorganic nutrients in the upper waters of a lake are unpredictable due to interactions with biota and organic factions (Toetz et al. 1972; Fast 1975). For example, aeration of Lake Roberts during June did not prevent a bloom of Anabaena, and total phosphate dropped throughout the lake, probably because of uptake by the algae (R.S. Kerr Research Center 1970; McNall 1971). During July however, aeration was followed by a massive die-off of Anabaena, perhaps due to a period of intense cloud cover and nutrient depletion. A rise in total phosphate accompanied the algal population crash. Artificial circulation often elevates total phosphorus levels by resuspension of organic detritus from the bottom or maintenance of dead cells in suspension (Hooper et al. 1953; Fast 1971a; Haynes 1973; Wirth and Dunst 1967). A fraction of this detritus will be liable to decomposition and subsequent release of inorganic forms of phosphorus will occur. Robinson et al. (1969) attributed an increase of organic nitrogen in Boltz Lake and Falmouth Lake to release of celluar contents by dead algae as they lysed or broke apart due to mixing. Finally, excretion of phosphorus by zooplankton may be an important recycling mechanism within the epilimnion (Devol 1979).

BIOLOGICAL MECHANISMS

An effective destratification often causes a dramatic shift in species composition of the phytoplankton community, from dominance by one or a few species of blue-greens to predominately an assemblage of green algae (Table 1). Fortunately, green algae remain dispersed in the water without forming nuisance "scums" on the surface as many blue-greens do. Moreover, zooplankton readily graze on green algal species, whereas they reject the inedible and sometimes toxic blue-greens or grow poorly on them (Arnold 1971; Porter 1973; Webster and Peters 1978). On the other hand, some gelatinous greens actually profit from passage through the gut of a Daphnia (Porter 1975).

King (1970) suggested that blue-green algae dominate the plankton of enriched lakes because of their efficiency in taking up CO_2 at the low ambient concentrations and high pH of these waters. Presumably, their ability to fix nitrogen, regulate vertical position, and avoid being eaten by grazers contribute to the competitive advantage of blue-greens over other algae.

Shapiro(1973;Shapiro et al.1975,1977) has induced the blue-green to green shift in experimental enclosures by adding CO_2 or HCl, both of which lower the pH of the water. Moreover, addition of NO_3^- and $PO_4^{\equiv}$ facilitates the shift. Since the blue-greens decline precipitously before the greens begin growing rapidly, Shapiro et al. (1975, 1977) suggest that the shift is mediated by the action of cyanophages, viruses specific to blue-green algae (Shilo 1971; Lindmark in Shapiro 1979), rather than by a direct competitive replacement. At high pH, cyanophages are inhibited, but when pH is lowered, they are capable of lysing blue-greens. Indeed, the release of large quantities of $PO_4^{\equiv}$ and NH_3 to the water after the sudden decline of blue-greens in the enclosures suggests that lysis is occurring.

Destratification essentially mimics Shapiro's experimental treatments by adding CO_2 and nutrients to the surface waters through: 1) mixing of hypolimnetic CO_2 and nutrients into the surface layer, 2) recarbonation of waters by atmospheric exchange, and 3) decreasing the ratio of primary production to respiration through deepening of the mixed layer. In experimental enclosures, a change in algal species composition occurs only at pH values less than 8.5, and the results are unpredictable between pH 7.5 and 8.5 (Shapiro et al. 1975, 1977). Whether or not artificial circulation results in a shift from blue-green algae to green algae apparently depends on the effect of mixing upon pH in the upper waters. Although the results are not clear-cut, lakes where the ratio of green algae to blue-green algae increased following circulation also showed a significant decrease in pH, whereas pH stayed the same or increased in mixing experiments that failed to produce the shift to greens or even stimulated growth of blue-green algae (Table 3). Where pH remained high after treatment, perhaps addition of CO_2 through circulation couldn't satisfy algal demands for CO_2 due to stimulation of photosynthesis by recycling of hypolimnetic nutrients (Shapiro et al. 1975).

In Kezar Lake during 1969, mixing caused a temporary rise in pH, but after 20 days of aeration, the pH dropped from 9.0 to 7.1, and at

TABLE 3. EPILIMNETIC pH CHANGES ASSOCIATED WITH ARTIFICIAL CIRCULATION

Lake	Reference	Direction of Change	pH Values	
			Before	After
Group I[a]				
Cline's Pond	Malueg et al. 1971	-	6.2-9.6[c]	6.4-7.2
University Lake	Weiss and Breedlove 1973	-	7.6[d]	7.3,7.0
Kezar Lake	N.H.W.S.P.C.C. 1971 Haynes 1973	1968 -	9.4	6.7
	N.H.W.S.P.C.C. 1971 Haynes 1973	1969 +	6.6	9
Stewart Hollow	Irwin et al. 1966	-	6.8	5.5
	Irwin et al. 1966	-	6.8	6.5
Cladwell Lake	Irwin et al. 1966	0	7.3	7.0-7.5
Pine Lake	Irwin et al. 1966	0	6.9-7.2	6.7-7.1
Vesuvius Lake	Irwin et al. 1966	-	6.8-7.3	6.8-7.0
Buchanan Lake	Brown et al. 1971	-	7.1	6.7
Group II[b]				
Parvin Lake	Lackey 1972	0	6.6-7.2[d]	6.7-7.2
Test Res. I & II	Knoppert et al. 1970	0?	?	>9
Starodworski Lake	Lossow et al. 1975	-	9.0-9.4[d]	7.3-8.6
Lake Calhoun	Shapiro and Pfannkuch 1973	0	8.0-8.5[d]	8.0-8.5
Ham's Lake	Steichen et al. 1974	1973 -	8.5	7.5
	Toetz 1977	1975 0	>8	>8
Arbuckle Lake	Toetz 1977	1975 -	7.71[d]	7.39
	Toetz 1979	1977 0	~7.5[d]	~7.5
Lake Catharine	Kothandaraman et al. 1979	0	>8[d]	>8
Hyrum Res.	Drury et al. 1975	±	7.8-8.9[d]	7.2-9.2
El Capitan Res.	Fast 1968	0	7.5-8.6[d]	7.7-8.3

[a] Group I = Lakes in which the ratio of green algae to blue-green algae increased after treatment

[b] Group II = Lakes in which the ratio of green algae to blue-green algae decreased or stayed the same after treatment

[c] Control section

[d] Control year, summer values

least a small increase in the ratio of greens to blue-greens ensured (N.H.W.S.P.C.C. 1971). Destratification by pumping hypolimnetic water to the surface maintained relatively low pH in the epilimnia of four Ohio lakes and prevented the usual fall blooms of blue-green algae (Irwin et al. 1966).

Although mixing caused a temporary decrease of epilimnetic pH in Ham's Lake (1973 experiment) and Starodworski Lake (Poland), the pH remained above 7.3 in both cases, failing to produce a shift from blue-green algae to green algae (Tables 2 and 3). In Hyrum Reservoir, where aeration caused microstratification and a reduction in mixed depth, pH of the surface waters rose sharply to 9.2 during a bloom of Aphanizomenon (Drury et al. 1975). Partial mixing in Arbuckle Lake, El Capitan Reservoir and Lake Catherine generated little change in pH and no apparent shifts in algal species composition.

BENEFITS/ADVERSE EFFECTS AND TECHNICAL PROBLEMS

The following outline summarizes some of the important considerations benefits and potential adverse effects associated with lake mixing. This summary includes hypolimnion aeration and consideration of higher trophic levels although they were not previously considered.

TECHNICAL PROBLEMS

Artificial Circulation

1. Placement of air release. If the air diffuser is located too far above the lake bottom, an anaerobic zone will persist below the air release depth.

2. Undersizing the system. When the system capacity is undersized with respect to the lake volume and area, an incomplete mix will result. In the case of a Garton pump or similar mechanical device located at the lake surface, the thermocline may be lowered, but an anoxic zone would persist near the lake bottom. If an air diffuser system is undersized, microstratification at the lake surface will encourage algal blooms. With any system, horizontal mixing will be limited in very large lakes when only one device is used.

3. Oversizing the system. If artificial mixing is too vigorous, sediments may be stirred and resuspended in the water column.

4. Oxygen depletion. When a lake is destratified too quickly after a long period of anoxia, mixing of hypolimnetic waters and bottom muds high in BOD into the surface layers may cause O_2 depletion throughout the lake and a fish-kill.

Hypolimnetic Aeration

1. Undersized aeration capacity. By underestimating the oxygen consumption rate in the hypolimnion or by overestimating the rate of oxygen dissolution by the system, the aerator may provide insufficient oxygen.

2. Unintentional thermal destratification. Side stream pumping of pure O_2 may mix the lake or cause significant warming of the hypolimnion if the discharge velocity is high. Water leakage through the vertical tower of a full air lift system will cause similar problems.

Assuming an effective application of techniques, i.e. sufficient oxygenation by hypolimnetic aeration or complete lake mixing in the case of artificial circulation, aeration/circulation will produce some or all of the following benefits and adverse impacts.

Improvement of Water Quality

1. Both artificial circulation and hypolimentic aeration can provide adequate aeration, although circulation does so more rapidly. Either technique minimizes taste, odor and corrosion problems by oxygenating bottom waters, raising their pH and lowering concentrations of reduced compounds. Hypolimnetic aeration maintains a cold water resource as well.

2. Artificial circulation generally reduces the temperature of the surface water and lowers evaporation rates.

3. As long as sediment stirring is avoided, enhancement of water clarity can be expected when aeration/circulation distributes algae throughout all depths and controls blooms.

Control of Nuisance Algae

Figure 2 summarizes the mechanisms underlying the beneficial effects of artificial circulation on phytoplankton populations.

1. A shift from blue-green algae to green algae will probably follow artificial circulation when pH declines to 7.5 or below resulting in "activation of cyanophages. The pH changes as hypolimnetic CO_2 is mixed into the surface waters and as algal uptake of CO_2 falls due to a reduction in light availability.

2. The abundance of blue-green algae decreases as vertical profiles are disrupted and cells are subjected to changes in light regimes and hydrostatic pressure.

3. The increases of mixed depth and suspended silt will probably induce light limitation of peak algal

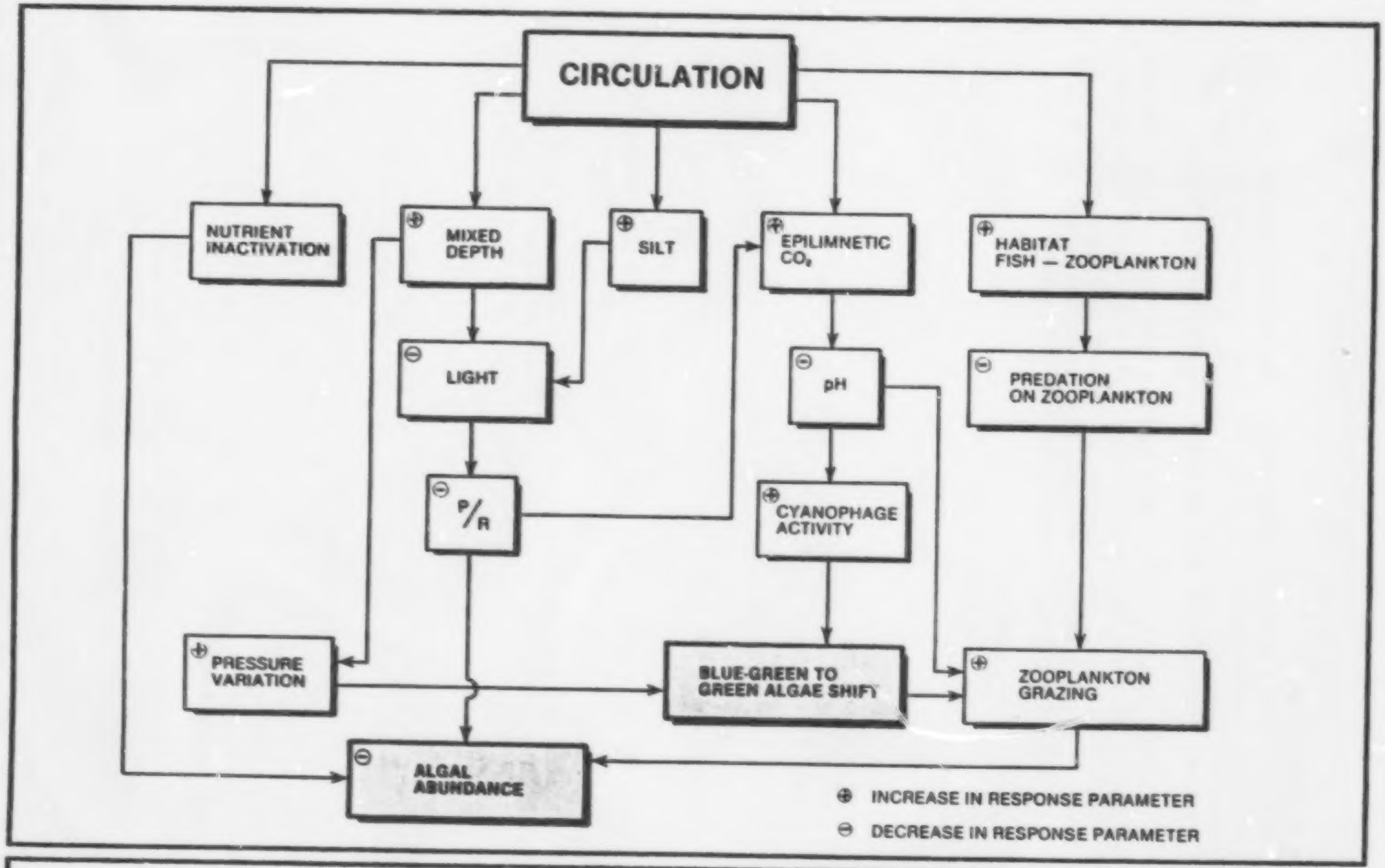

CIRCULATION
NUTRIENT INACTIVATION
⊕ MIXED DEPTH
⊕ SILT
⊕ EPILIMNETIC CO₂
⊕ HABITAT FISH — ZOOPLANKTON
⊖ LIGHT
⊖ pH
⊖ PREDATION ON ZOOPLANKTON
⊖ P/R
⊕ CYANOPHAGE ACTIVITY
⊕ PRESSURE VARIATION
BLUE-GREEN TO GREEN ALGAE SHIFT
⊕ ZOOPLANKTON GRAZING
⊖ ALGAL ABUNDANCE
⊕ INCREASE IN RESPONSE PARAMETER
⊖ DECREASE IN RESPONSE PARAMETER

FIGURE 2
BENEFICIAL EFFECTS OF ARTIFICIAL CIRCULATION
ON PHYTOPLANKTON (ADAPTED FROM SHAPIRO 1979)

biomass, especially in deep lakes. However, the prediction of a reduction in algal crop depends on maintenance of a uniform vertical distribution or nearly so; moreover, if algae are limited by nutrients rather than light before treatment, a moderate increase in mixed depth may actually cause greater algal growth. In any event, a given change in mixed depth will usually produce a larger change of algal biomass in eutrophic lakes than in oligotrophic lakes.

4. Artificial circulation stimulates sediment decomposition, resulting in mineralization of organic fractions and consolidation of the sediments. In the long-term, treatment probably reduces internal loading of nutrients by oxygenating hypolimnetic waters and surficial profundal sediments, creating a sink for phosphorus compounds. However, the importance of mixing, sediment composition and decomposition rates in determining nutrient exchange across the mud-water interface demands further investigation.

5. At present, there is no evidence that hypolimnetic aeration will control algal blooms.

6. Artificial circulation effectively increases the grazing pressure on phytoplankton by shifting the community toward more edible forms and by elevating the abundance of large zooplankton.

7. The relative importance of light, nutrients and grazing in controlling algal biomass will undoubtedly vary among sites; this accounts for some variation in the responses of different communities to treatment.

Effects on Benthic Macroinvertebrates

1. Aeration/circulation may produce changes in benthic organisms without corresponding shifts in planktonic biomass and production, e.g. Ham's Lake experiment (1976).

2. The distribution and abundance of benthic macroinvertebrates increases following aeration/circulation. Changes in abundance may be greater after hypolimnetic aeration than they are with circulation because the latter elevates water temperatures, causing rapid turnover of populations and earlier emergence of benthic insects.

3. Aeration/circulation induces a shift in trophic structure of the macroinvertebrate community, with infaunal detritivores (mainly chironomids, oligochaetes) replacing predatory insects (Chaoborus) which exploit zooplankton prey.

Improvement of Fisheries

1. Aeration/circulation prevents winter-kill and summer-kill of fishes by alleviating anoxic conditions and eliminating toxic gases.

2. Artificial circulation expands habitat for warmwater fishes. In northern lakes where surface temperatures remain below 22°C throughout the summer, mixing should create or expand habitat for cold-water fishes.

   Hypolimnetic aeration creates habitat for cold-water fishes and fosters a two-story fisher.

3. By enhancing their habitat and food supply, aeration/circulation has great potential for improving growth of fishes, environmental carrying capacity, and overall yield. However, little evidence exists for these long-term benefits. In addition, an increase in recreational yield may result simply from catch per unit effort due to concentration of fishes near the aeration device.

4 Accrual of maximum fisheries benefits will be achieved by treatment before the development of full stratification.

Water Quality

1. Destratification facilitates a temporary recycling of nutrients by mixing hypolimnetic waters into the trophogenic zone.

2. Artificial circulation raises suspended silt levels by slowing rates of sedimentation and possibly increasing sediment resuspension. Often, water transparency decreases due to silt load and temporary algal blooms.

3. Hypolimnetic aeration has no known adverse impacts on water quality.

Nuisance Algae

Figure 3 summarizes the mechanisms producing undesirable changes in phytoplankton communities after artificial circulation/destratification.

1. The recycling of hypolimnetic nutrients and elevation of total posphorus by artificial destratification may stimulate a temporary algal bloom.

2. An immediate dilution of algae following destratification effectively lowers zooplankton filtering rates and the intensity of grazing on phytoplankton. This may cause short-term increases in algal biomass before zooplankton populations grow to post-treatment levels.

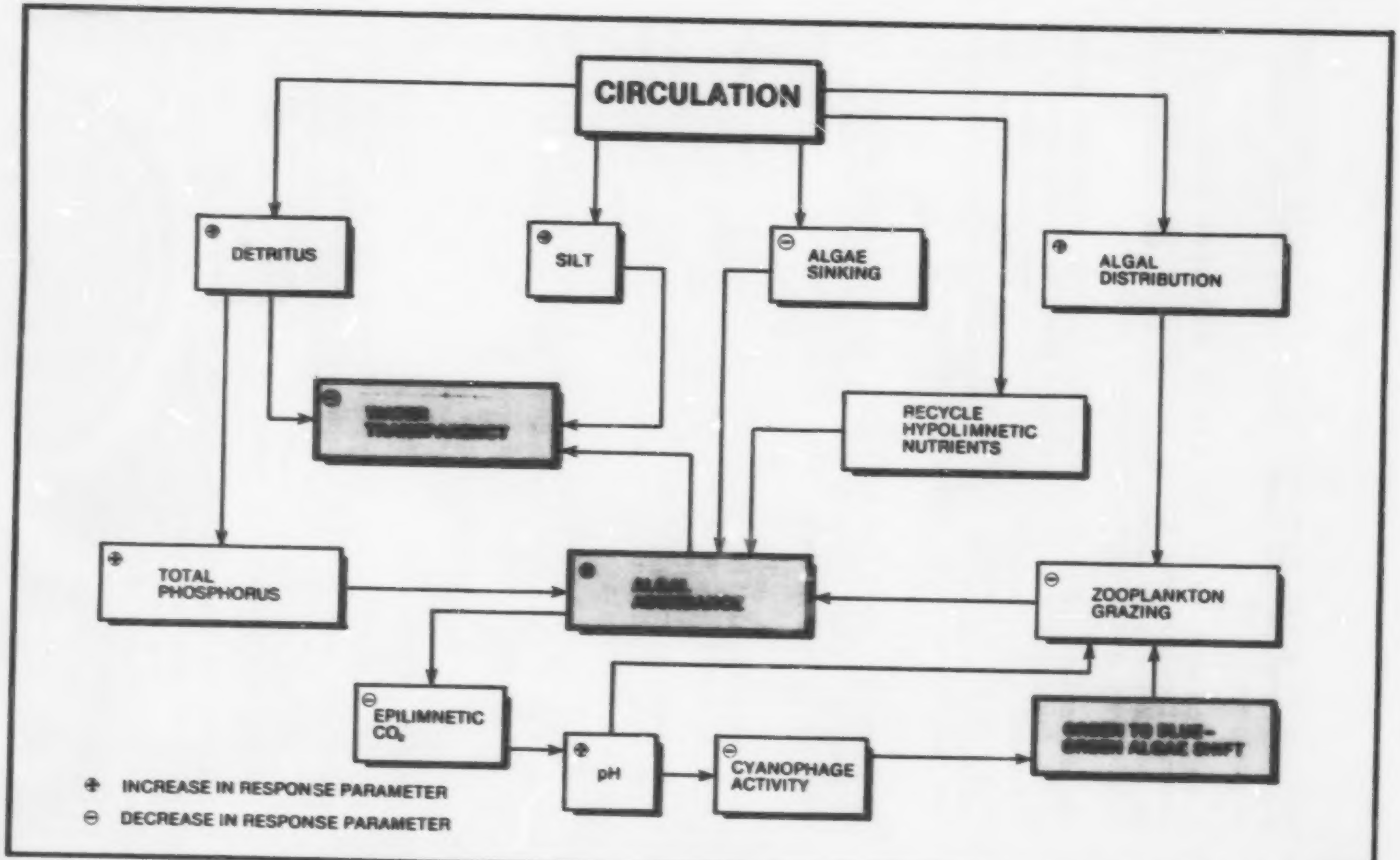

CIRCULATION
⊕ DETRITUS
⊕ SILT
⊖ ALGAE SINKING
⊕ ALGAL DISTRIBUTION
⊖ WATER TRANSPARENCY
RECYCLE HYPOLIMNETIC NUTRIENTS
⊕ TOTAL PHOSPHORUS
⊕ ALGAL ABUNDANCE
⊖ ZOOPLANKTON GRAZING
⊖ EPILIMNETIC CO₂
⊕ pH
⊖ CYANOPHAGE ACTIVITY
GREEN TO BLUE-GREEN ALGAE SHIFT
⊕ INCREASE IN RESPONSE PARAMETER
⊖ DECREASE IN RESPONSE PARAMETER

FIGURE 3
SOME ADVERSE IMPACTS OF ARTIFICIAL CIRCULATION AND THEIR ROLE IN PROMOTING BLUE-GREEN ALGAE BLOOMS (ADAPTED FROM SHAPIRO 1979)

3. Decline of algal sinking rates following artificial destratification will favor heavy algae without buoyancy adaptations.

4. A temporary rise in algal biomass following destratification may favor blue-green algae by depleting CO_2 and keeping pH levels high. In turn, the intensity of zoöplankton grazing is effectively reduced.

5. The assemblage of blue-green algae and the alternate green algal association represent alternative stable states of the community. Maintenance of blue-green algae following some destratification experiments probably results from initial stimulation of algal growth by nutrient recycling and failure to lower surface pH values.

Macrophytes

1. In lakes with shallow littoral shelves, macrophytes may invade or expand to nuisance levels if water transparency improves following artificial circulation.

Fisheries

1. Aeration/circulation may raise N_2 gas concentrations to levels capable of inducing gas bubble disease in fish.

2. Artificial circulation may eliminate habitat for coldwater fishes in southern lakes where metalimnetic populations existed before treatment.

3. Regardless of precautionary measures, artificial destratification involves some risk of extensive oxygen depletion and fish-kills.

RECOMMENDATIONS

SYSTEM DESIGN AND APPLICATION

1. Aeration/circulation is recommended as an inexpensive, efficient restoration technique, potentially useful for treating the symptoms of eutrophication when alternative management schemes, such as the control of nutrient influx, are deemed too costly or technically unfeasible.

2. Release of compressed air or a mechanical pump will achieve adequate mixing in shallow and moderately deep lakes. However, a combination of a surface pump and a bottom aerator will probably give the best results in very deep lakes, especially where intense surface heating could cause thermal microstratification and associated algal blooms if only air diffussion is used.

3. The full-air lift design is recommended for hypolimnetic aeration because it is the least costly system to construct, install and operate and almost twice as efficient as other systems in terms of pounds of oxygen dissolved per kilowatt-hour. However, each system has unique properties that might be considered relevant for a prospective aeration site. Injection of pure oxygen should be considered as an alternative to aeration when a potential for N_2 supersaturation exists and downstream releases are inevitable.

4. Air diffusers should be located near the lake bottom to avoid development of anoxia in the deepest portion of the lake basin. Diffusers should be oriented such that released air does not stir the surficial sediments directly.

5. Approximately 9.2 m^3/min of air per 10^6 m^2 of lake surface (= 30 SCFM per 10^6 ft^2) is recommended to attain good mixing. Unless necessary to achieve an adequate mix, more intense aeration should be avoided because of problems resulting from resuspension of bottom sediments.

   Hypolimnetic aeration rates should be determined by the method outlined in Lorenzen and Fast (1977).

6. Unless an elevation of algal productivity is desired, artificial circulation techniques should be applied before full development of thermal stratification to avoid post-treatment recycling of nutrients accumulated in the hypolimnion.

7. When the hypolimnion is already anoxic, aeration might be started slowly and gradually intensified to force nutrient precipitation and oxygenation of the bottom layer and avoid mixing high BOD waters into the surface stratum. This might avert possible oxygen depletion throughout the lake and a subsequent fish-kill.

IMPROVEMENT OF WATER QUALITY

1. When a cold water supply is needed, and control of algal blooms is not critical, hypolimnetic aeration is recommended. On the other hand, artificial circulation is preferred whenever limitation of algal biomass is desirable, oxygenation of the metalimnion is required, or loss of cool water is acceptable. Although untested, the combination of a hypolimnetic aerator with a mid-water mixing device might be used to lower the themocline and oxygenate the entire lake while maintaining cold bottom water.

2. Either aeration/circulation method is recommended for use by water supply managers seeking to alleviate "taste and odor" problems resulting from high concentrations of Fe, Mn, H_2S and other chemicals which accumulate in the anoxic hypolimnion.

3. When water transparency is a primary amenity, artificial circulation should be applied cautiously to avoid resuspension of bottom sediments and algal blooms.

CONTROL OF NUISANCE ALGAE

Although aeration/circulation techniques cannot be considered a "cure-all" for algal problems, the following recommendations should increase the likelihood of bloom control while reducing the risk of undesirable results.

1. Hypolimnetic aeration should be considered as a method for bloom control only in cases where internal loading of nutrients is high relative to external loading, and blooms occur following natural destratification in autumn or during early spring as a result of prior recycling of hypolimnetic nutrients.

2. Mixing techniques are recommended when the nuisance species is known to be sensitive to disruption of its vertical profile and variable hydrostatic pressures. Usually these are buoyant blue-green algae, such as *Anabaena* spp. and *Oscillatoria* spp., with depth-specific light and nutrient requirements.

3. When a lasting reduction of algal standing crop is desired, an evaluation of limiting mechanisms should preceed treatment (cf. Lorenzen and Mitchell 1975; Lorenzen and Fast 1977). Mixing techniques should be applied only in lakes where algal biomass is limited by low light levels or could be limited by reduced light availability resulting from an increase in mixed depth. Although a temporary reduction in algal biomass and a shift in species composition may follow mixing of a shallow lake, artificial circulation will probably not control total algal growth in shallow lakes.

ENHANCEMENT OF FISHERIES

1. Artificial circulation is appropriate for northern lakes where surface waters would remain below 22°C during summer allowing distribution of both cold-water and warm-water fishes throughout the lake.

2. Hypolimnetic aeration is recommended for southern lakes

where high water temperatures in the epilimnion and metalimnion along with anoxic conditions in the hypolimnion otherwise preclude establishment of a coldwater fisheries.

3. Hypolimnetic aeration is recommended when improvement of fisheries is the only consideration, e.g. when control of algal blooms is unnecessary.

FUTURE RESEARCH

1. Observational methods and experimental designs could be greatly improved. Ideally, at least two years of pretreatment data are required for proper evaluation of the effects of any perturbation on biological communities in lakes. Within-lake controls such as large enclosures or unaffected stations are also desirable. Chemical observations should focus on the flux of nutrients between various compartments of the system, especially sediment-water exchange, in addition to standing quantity within each compartment.

2. A team research approach is desirable in assessing the impact of aeration/circulation on lake ecology.

3. Integration of mathematical models predicting peak algal biomass (e.g. Lorenzen and Mitchell 1975) with conceptual models explaining shifts in algal species composition (Shapiro et al. 1975; Shapiro 1979) could form a basis for a priori hypotheses about community responses amenable to experimental testing. A systems analysis approach to lake ecosystems could provide a holistic view necessary to understand the complex response mechanisms operating during aeration/circulation treatment.

4. Long-term responses of lake systems to treatment need to be examined. Organisms with long generation times and slow turnover rates (e.g. fishes) may require up to five years or more to reach equilibrium growth and carrying capacity.

5. A general area requiring additional research concerns how trophic structure and species composition of communities determines responses to aeration/circulation.

6. The possibility that nitrogen supersaturation resulting from aeration could induce gas-bubble disease in fish needs to be investigated further.

REFERENCES

Ambuhl, H. 1967. Discussion of impoundment destratification by mechanical pumping. (W. H. Irwin, J. M. Symons, and G. G. Robeck). J. Sanit. Eng. Div., Amer. Soc. Civil Eng. 93:141-143.

American Water Works Association. 1971. Artificial destratification in reservoirs. Committee Report 63:597-604.

Andersson, G., H. Berggren, G. Cronberg, and C. Gelin. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59:9-15.

Arnold, D. E. 1971. Ingestion, assimilation, survival, and reproduction by Daphnia pulex fed seven species of blue-green algae. Limnol. Oceanogr. 16:906-920.

Barnes, M. D. and B. L. Griswold. 1975. Effects of artificial nutrient circulation on lake productivity and fish growth. Speciality Conference on Lake Reaeration Research, Amer. Soc. Civil Eng., Gatlinburg, Tennessee.

Barnett, R. H. 1975. Case study of reaeration of Casitas Reservoir. Speciality Conference on Lake Reaeration Research, Amer. Soc. Civil Eng., Gatlinburg, Tennessee.

Bartell, S. M., and J. F. Kitchell. 1978. Seasonal impact of planktivory on phosphorus release by Lake Wingra zooplankton. Verh. Internat. Verein. Limnol. 20:466-474.

Bengtsson, L., and H. Berggren. 1972. The bottom fauna in an oil contaminated lake. Ambio. 1:141-144.

Bengtsson, L., H. Berggren, O. Meyer, and B. Verner. 1972. Restaurering av sjoar med kulturbetingat hypolimniskt syrgasdeficit. Limnologiska Institutionen, Lunds Universitet Centrala Fysiklaboratoriet, Atlas Copco AB. (as quoted in Dunst et al. 1974).

Bengtsson, L., and C. Gelin. 1975. Artificial aeration and suction dredging methods for controlling water quality. Proc. Symp. on Effects of Storage on Water Quality, Water Res. Centre, Medmenham, England.

Bernhardt, H. 1967. Aeration of Wahnbach Reservoir without changing the temperature profile. J. Amer. Water Works Assoc. 9:943-964.

Bernhardt, H. 1974. Ten years' experience of reservoir aeration. Seventh Internat. Conf. on Water Pollut. Res., Paris.

Biederman, W. J., and E. E. Fulton. 1971. Destratification using air. Amer. Water Works Assoc. 63:462-466.

Blahm, T. H., et al. 1976. Gas supersaturation research, National Marine Fisheries Service Prescott Facility - 1971 to 1974. Pages 11-19 *in* D. H. Fickeisen and M. J. Schneider, eds. Gas bubble disease. Energy Res. Dev. Admin. (as quoted by Fast 1979).

Bowles, L. G. 1972. A description of the spatial and temporal variations in species composition and distribution of pelagic net zooplankton in the central pool of Eufaula Reservoir, Oklahoma, with comment on forced aeration destratification experimentation. Trans. Kansas Acad. Sci. 75:156-173.

Bradshaw, A. S. 1964. The crustacean zooplankton picture: Lake Erie 1939-49-59; Cayuga 1910-51-61. Verh. Internat. Verein. Limnol. 15:700-708.

Brezonik, P., J. Delfino, and G. Fred Lee. 1969. Chemistry of N and Mn in Cox Hollow Lake, Wisconsin, following destratification. J. Sanit. Eng. Div., Amer. Soc. Civil Eng. 95:929-940.

Brooks, J. L. 1969. Eutrophication and changes in the composition of the zooplankton. Pages 236-255 *in* National Academy of Sciences, Proc. Symp. on *Eutrophication: Causes, Consequences, Correctives*. Washington, D.C.

Brown, D. J., T. G. Brydges, W. Ellerington, J. J. Evans, M. F. P. Michalski, G. G. Hitchin, M. D. Palmer, and D. M. Veal. 1971. Progress report on the destratification of Buchanan Lake. Ont. Water Res. Comm., AID for Lakes Program (Artificially Induced Destratification).

Brynildson, O. M., and S. L. Serns. 1977. Effects of destratification and aeration of a lake on the distribution of planktonic Crustacea, yellow perch and trout. Wisc. Dept. Natur. Resour. Tech. Bull. No. 99. 22 pp.

Confer, J. L., R. A. Tubb, T. A. Haines, P. Blades, W. Overholtz, and C. Willoughby. 1974. Hypolimnetic aeration without destratification: Zooplankton response in three lakes with normal clinograde oxygen curves. Presented at the 37th Annual Meeting Amer. Soc. Limnol. Oceanogr., Univ. Washington, Seattle.

Davis, R. B., D. L. Thurlow, and F. E. Brewster. 1975. Effects of burrowing tubificid worms on the exchange of phosphorus between lake sediment and overlying water. Verh. Internat. Verein. Limnol. 19:382-394.

DeBernardi, R., and G. Giussani. 1978. Effect of mass fish mortality on zooplankton structure and dynamics in a small Italian lake (Lago di Annone). Verh. Internat. Verein. Limnol. 20:1045-1048.

DeMarte, J. A., and R. T. Hartman. 1974. Studies on absorption of ^{32}P, ^{59}Fe, and ^{45}Ca by water-milfoil (*Myriophyllum exalbescens* FERNALD). Ecology 55:188-194.

Devol. A. H. 1979. Zooplankton respiration and its relation to plankton dynamics in two lakes of contrasting trophic state. Limnol. Oceanogr. 24:893-905.

Drury, D. D., D. B. Porcella, and R. A. Gearheart. 1975. The effects of artificial destratification on the water quality and microbial populations of Hyrum Reservoir. Utah Wat. Res. Lab. PRJEW 011-1.

Dunst, R. C., S. M. Born, P. D. Uttormark, S. A. Smith, S. A. Nichols, J. O. Peterson, D. R. Knauer, S. L. Serns, D. R. Winter, and T. L. Wirth. 1974. Survey of lake rehabilitation techniques and experiences. Wisconsin Dept. of Natur. Resour., Tech. Bull. No. 75.

Fast, A. W. 1968. Artificial destratification of El Capitan Reservoir by aeration. Part 1: Effects on chemical and physical parameters. Calif. State Dept. of Fish and Game. Fish. Bull. 141.

Fast, A. W. 1971a. The effects of artificial aeration on lake ecology. Water Pollut. Control Res. Ser. 16010 EXE 12/71. U.S. Environmental Protection Agency.

Fast, A. W. 1971b. Effects of artificial destratification on zooplankton depth distribution. Trans. Amer. Fish. Soc. 100:355-358.

Fast, A. W. 1973a. Effects of artificial destratification on primary production and zoobenthos of El Capitan reservoir, California. Water Resour. Res. 9:607-623.

Fast, A. W. 1973b. Effects of artificial hypolimnion aeration on rainbow trout (*Salmo gairdnerii* Richardson) depth distribution. Trans. Amer. Fish. Soc. 102:715-722.

Fast, A. W. 1975. Artificial aeration and oxygenation of lakes as a restoration technique. Symposium on the Recovery of Damaged Ecosystems, Virginia Polytechnic Institute and State University, Blacksburg.

Fast, A. W. 1979a. Artificial aeration as a lake restoration technique. Proc. Natl. Conf. Lake Restoration. U.S. Environ. Prot. Agency.

Fast, A. W. 1979b. Nitrogen gas supersaturation during artificial aeration at Lake Casitas, California. Prog. Fish. Cult. 41:153-154.

Fast, A. W., and J. A. St. Amant. 1971. Nighttime artificial aeration of Puddingstone Reservoir, Los Angeles County, California. Calif. Fish Game 57:213-216.

Fast, A. W., and M. W. Lorenzen. 1976. Synoptic survey of hypolimnetic aeration. J. Environ. Eng. Div., Amer. Soc. Civil Eng. 102:1161-1173.

Fast, A. W., V. A. Dorr, and R. J. Rosen. 1975a. A submerged hypolimnion aerator. Water Resour. Res. 11:287-293.

Fast, A. W., W. J. Overholtz, and R. A. Tubb. 1975b. Hypolimnetic oxygenation using liquid oxygen. Water Resour. Res. 11:294-299.

Fast, A. W., M. W. Lorenzen, and J. H. Glenn. 1976. Comparative study with costs of hypolimnetic aeration. J. Environ. Eng. Div., Amer. Soc. Civil Eng. 102:1175-1187.

Fast, A. W., B. Moss, and R. G. Wetzel. 1973. Effects of artificial aeration on the chemistry and algae of two Michigan lakes. Water Resour. Res. 9:624-647.

Fogg, G. E., and A. E. Walsby. 1971. Buoyancy regulation and the growth of planktonic blue-green algae. Mitt. Internat. Verein. Limnol. 19:182-188.

Gallepp, G. W., J. F. Kitchell, and S. M. Bartell. 1978. Phosphorus release from lake sediments as affected by chironomids. Verh. Internat. Verein. Limnol. 20:458-465.

Gannon, J. E., and R. S. Stemberger. 1978. Zooplankton (especially crustaceans and rotifers) as indicators of water quality. Trans. Amer. Micros. Soc. 97:16-35.

Garrell, M. H., J. C. Confer, D. Kirchner, and A. W. Fast. 1977. Effects of hypolimnetic aeration on nitrogen and phosphorus in a eutrophic lake. Water Resour. Res. 13:343-347.

Garton, J. E. 1978. Improve water quality through lake destratification. Water Wastes Eng. 15:42-44.

Garton, J. E., and R. E. Punnett. 1978. Water quality improvement in small ponds. Res. Proj. Tech. Completion Rept. A-065-OKLA, Oklahoma Water Resour. Res. Inst.

Garton, J. E., R. G. Strecker, and R. C. Summerfelt. 1978. Performance of an axial flow pump for lake destratification. W. A. Rogers, ed. Proc. 13th Annual Conf. S.E. Assoc. Fish Wildl. Agencies. pp. 336-346.

Garton, J. E., R. C. Summerfelt, D. Toetz, J. Wilhm, and H. Jarrell. 1977. Physiochemical and biological conditions in two Oklahoma reservoirs undergoing artificial destratification. Oklahoma Water Resour. Res. Inst. Rept. No. REC-ERC-77-6.

Gebhart, G. E., and M. D. Clady. 1977. Effects of mechanical mixing in reservoirs on seasonal and annual growth rates of fishes. Tech. Completion Rept. A-069-OKLA, Oklahoma Water Resour. Res. Inst.

Gebhart, G. E., and R. C. Summerfelt. 1976. Effects of destratification on depth distribution of fish. J. Environ. Eng. Div., Amer. Soc. Civil Eng. 102:1215-1228.

Graetz, D. A., D. R. Kenney, and R. B. Aspiras. 1973. The status of lake sediment-water systems in relation to nitrogen transformations. Limnol. Oceanogr. 18:908-917.

Halsey, T. G. 1968. Autumnal and over-winter limnology of three small eutrophic lakes with particular reference to experimental circulation and trout mortality. J. Fish. Res. Bd. Canada 25:81-99.

Halsey, T. G., and D. M. Galbraith. 1971. Evaluation of two artificial circulation systems used to prevent trout winter-kill in small lakes. British Columbia Fish Wildl. Branch, Fish. Manage. Publ. No. 16.

Halsey, T. C., and S. J. MacDonald. 1971. Experimental trout introduction and artificial circulation of Yellow Lake, British Columbia. B.C. Fish Wildl. Branch, Fish. Manage. Rep. No. 63.

Haney, J. F. 1973. An in-situ examination of the grazing activities of natural zooplankton communities. Arch. Hydrobiol. 72:87-132.

Hargrave, B. T. 1969. Epibenthic algae production and community respiration in the sediments of Marion Lake. J. Fish Res. Bd. Canada 26:2003-2026.

Hasler, A. D. 1957. Natural and artificially (air-ploughing) induced movement of radioactive phosphorus from the muds of lakes. Proc. UNESCO Internat. Conf. Radioisotopes Sci. Research, Paris. 4:658-675.

Haynes, R. C. 1973. Some ecological effects of artificial circulation on a small eutrophic lake with particular emphasis on phytoplankton. I. Kezar Lake experiment. Hydrobiologia 43:463-504.

Heberger, R. F., and J. B. Reynolds. 1977. Abundance, composition, and distribution of crustacean zooplankton in relation to hypolimnetic oxygen depletion in west central Lake Erie. U.S. Fish. Wildl. Serv. Tech. Pap. 93. 18 pp.

Heisey, D., and K. G. Porter. 1977. The effect of ambient oxygen concentration on filtering and respiration rates of Daphnia galeata mendotae and Daphnia magna. Limnol. Oceanogr. 22:839-845.

Hooper, F. F., R. C. Ball, and H. A. Tanner. 1953. An experiment in the artificial circulation of a small Michigan Lake. Trans. Am. Fish. Soc. 82:222-241.

Hrbacek, J., M. Dvorakova, M. Korinek, and L. Prochazkova. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verh. Internat. Verein. Limnol. 14:192-195.

Hrbacek, J., B. Desortova, and J. Popovsky. 1978. Influence of the fishstock on the phosphorus-chlorophyll ratio. Verh. Internat. Verein. Limnol. 20:1624-1628.

Hutchinson, G. E. 1957. A treatise on limnology. John Wiley and Sons, Inc., New York. 1015 pp.

Inland Fisheries Branch. 1970. Effects of artificial destratification on distribution of bottom organisms in El Capitan Reservoir. Fish Bull. 148, California Department of Fish and Game.

Irwin, W. H., J. M. Symons, and G. G. Robeck. 1966. Impoundment destratification by mechanical pumping. J. Sanit. Eng. Div., Amer. Soc. Civ. Eng. 92(SA6):21-40.

Johnson, R. C. 1966. The effect of artificial circulation on production of a thermally stratified lake. Wash. Dept. Fish., Fish. Res. Pap. 2:5-15.

Kamp-Nielsen, L. 1974. Mud-water exchange of phosphate and other ions in undisturbed sediment cores and factors affecting the exchange rates. Arch. Hydrobiol. 73:218-237.

Kamp-Nielsen, L. 1975. Seasonal variation in sediment-water exchange of nutrient ions in Lake Esrom. Verh. Internat. Verein. Limnol. 19:1057-1065.

King, D. L. 1970. The role of carbon in eutrophication. J. Water Pollut. Control Fed. 42:2035-2051.

Knauer, D. R. 1975. The effect of urban runoff on phytoplankton ecology. Verh. Internat. Verein. Limnol. 19:893-903.

Knoppert, P. L., J. J. Rook, T. Hofker, and G. Oskam. 1970. Destratification experiments at Rotterdam. J. Amer. Water Works Assoc. 62:448-454.

Kobus, H. E. 1968. Analysis of the flow induced by air bubble system. Coastal Eng. Conf., London. 2:1016-1031.

Konopka, A., T. D. Brock, and A. E. Walsby. 1978. Buoyancy regulation by planktonic blue-green algae in Lake Mendota, Wisconsin. Arch. Hydrobiol. 83:524-537.

Kothandaraman, V., D. Roseboom, and R. L. Evans. 1979. Pilot lake restoration investigations: Aeration and destratification in Lake Catharine. Illinois State Water Survey.

Lackey, R. T. 1972. Response of physical and chemical parameters to eliminating thermal stratification in a reservoir. Water Res. Bull. 8:589-599.

Lackey, R. T. 1973a. Artificial reservoir destratification effects on phytoplankton. J. Water Pollut. Control. Fed. 45:668-673.

Lackey, R. T. 1973b. Effects of artificial destratification on zooplankton in Parvin Lake, Colorado. Trans. Am. Fish. Soc. 102:450-452.

Lackey, R. T. 1973c. Bottom fauna changes during artificial reservoir destratification. Water Res. 7:1349-1356.

Lane, P., and R. Levins. 1977. The dynamics of aquatic systems. 2. The effects of nutrient enrichment on model plankton communities. Limnol. Oceanogr. 22:454-471.

Langford, R. R. 1938. Diurnal and seasonal changes in the distribution of the limnetic Crustacea of Lake Nipissing, Ontario. Univ. Toronto, Biol. Ser. 45, Publ. Ont. Fish. Res. Lab., No. 56. 142 pp.

LaRow, E. J. 1970. The effect of oxygen tension on the vertical migration of *Chaoborus* larvae. Limnol. Oceanogr. 15:357-362.

Leach, L. E., W. R. Duffer, and C. C. Harlin, Jr. 1970. Induced hypolimnion aeration for water quality improvement of power releases. Water Pollut. Control Res. Ser. 16080. U.S. Environ. Prot. Agency.

Lehman, J. T., and C. D. Sandgren. 1978. Documenting a seasonal change from phosphorus to nitrogen limitation in a small temperate lake, and its impact on the population dynamics of *Asterionella*. Verh. Internat. Verh. Limnol. 20:375-380.

Likens, G. E., ed. 1972. Nutrients and eutrophication: The limiting-nutrient controversy. Amer. Soc. Limnol. Oceanogr., Spec. Symp. 1. 328 pp.

Linder, C. H., and P. Mercier. 1954. Etude comparative de la repartition du zooplankton au lac de Bret avant et apres rearation. Schweiz Zeitschr. Hydrol. 16:309-317.

Lorenzen, M. W., and A. W. Fast. 1977. A guide to aeration/circulation techniques for lake management. Res. Ser. EPA-600/3-77-004. U.S. Environ. Prot. Agency.

Lorenzen, M. W., and R. Mitchell. 1975. An evaluation of artificial destratification for control of algal blooms. J. Amer. Water Works Assoc. 67:373-376.

Lossow, K, A. Sikorowa, H. Drozd, A. Wuchowa, H. Nejranowska, M. Sobierajska, J. Widuto, and I. Zmyslowska. 1975. Results of research on the influence of aeration on the physico-chemical systems and biological complexes in the Starodworskie Lake obtained hitherto. Pol. Arch. Hydrobiol. 22:195-216.

Malueg, K. W., J. R. Tilstra, D. W. Schults, and C. F. Powers. 1971. Effect of induced aeration on stratification and eutrophication processes in an Oregon farm pond. Geophys. Monogr. Ser. 17:578-587.

McClintock, N. 1976. Effects of artificial destratification on zooplankton of two Oklahoma reservoirs. M.S. thesis, Okla. State Univ. 43 pp.

McCullough, J. R. 1974. Aeration revitalizes reservoir. Water and Sewage Works. 121:84-85.

McNall, W. J. 1971. Destratification of lakes. Federal AID project F-22-R-11, J of C-8, Job Program Report. 31 pp.

McNaught, D. C. 1978. Spatial heterogeneity and niche differentiation in zooplankton of Lake Huron. Verh. Internat. Verein. Limnol. 20:341-346.

Mercier, P. 1955. Aeration partielle sous-lacustrine d'un lac eutrope. Verh. Internat. Verein. Limnol. 10:294-297.

Mercier, P., and S. Gay. 1954. Effets de l'aeration artificielle sous-lacustre au lac de Bret. Schweizer z.f. Hydrol. 16:248-308.

Mercier, P., and J. Perret. 1949. Aeration station of Lake Bret. Monatsbull. Schweiz. Ver. Gas. u. Wasser-Fachm. 29:25.

Mortimer, C. H. 1941, 1942. The exchange of dissolved substances between mud and water in lakes. J. Ecol. 29:280-329, 30:147-201.

Mortimer, C. H. 1971. Chemical exchanges between sediments and water in the Great Lakes--Speculations on probable regulatory mechanisms. Limnol. Oceanogr. 16:387-404.

Murphy, G. I. 1962. Effects of mixing depth and turbidity on the productivity of freshwater impoundments. Trans. Amer. Fish. Soc. 91:69-76.

New Hampshire Water Supply and Pollution Control Commission. 1971. Algae control by mixing. Concord, New Hampshire. 103 pp.

Northcote, T. G., H. W. Lorz, and J. C. MacLeod. 1964. Studies on diel vertical movement of fishes in a British Columbia lake. Verh. Internat. Verein. Limnol. 15:940-946.

Northcote, T. G., C. J. Walters, and J. M. B. Hume. 1978. Initial impacts of experimental fish introduction on the macrozooplankton of small oligotrophic lakes. Verh. Internat. Verein. Limnol. 20:2003-2012.

Oglesby, R. T. 1977. Relationships of fish yield to lake phytoplankton standing crop, production and morphoedaphic factors. J. Fish. Res. Board, Canada 34:2271-2279.

Oskam, G. 1978. Light and zooplankton as algae regulating factors in eutrophic Biesbosch reservoirs. Verh. Internat. Verein. Limnol. 20:1612-1618.

Overholtz, W. J., A. W. Fast, R. A. Tubb, and R. Miller. 1977. Hypolimnion oxygenation and its effects on the depth distribution of rainbow trout (*Salmo gairdnerii*) and gizzard shad (*Dorosoma cepedianum*). Trans. Am. Fish. Soc. 106:371-375.

Pastorok, R. A. In press. Selection of prey by *Chaoborus* larvae: A review and new evidence for behavioral flexibility. Amer. Soc. Limnol. Oceangr., Spec. Symp. 3.

Porcella, D. B., J. S. Kumagai, and E. J. Middlebrooks. 1970. Biological effects on sediment-water nutrient interchange. J. Sanit. Eng. Div., Amer. Soc. Civil Eng. 96:911-926.

Porter, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature 244:179-180.

Porter, K. G. 1975. Viable gut passage of gelatinous green algae ingested by *Daphnia*. Verh. Internat. Verein. Limnol. 19:2840-2850.

Quintero, J. E., and J. E. Garton. 1973. A low energy lake destratifier. Trans. Am. Soc. Agr. Eng. 16:973-978.

Riddick, T. M. 1957. Forced circulation of reservoir waters yields multiple benefits at Ossining, New York. Water and Sewage Works 104:231-237.

Ridley, J. E. 1970. The biology and management of eutrophic reservoirs. Water Treat. Exam. 19:374-399.

Ridley, J. E., P. Cooley, and J. A. P. Steel. 1966. Control of thermal stratification in Thames Valley reservoirs. Proc. Soc. Water Treatment and Exam. 15:225-244.

Rieder, W. G. 1977. Wind powered artificial aeration of northern prairie lakes. Res. Proj. Tech. Completion Rept., North Dakota Water Resour. Res. Inst.

Robinson, E. L., W. H. Irwin, and J. M. Symons. 1969. Influence of artificial destratification on plankton populations in impoundments. Trans. Ky. Acad. Sci. 30:1-18.

R. S. Kerr Research Center. 1970. Induced aeration of small mountain lakes. Water Pollut. Control Res. Ser. 16080-11/70, U.S. Environ. Prot. Agency.

Rucker, R. 1972. Gas bubble disease: A critical review. Bur. Sport Fish. Wildl., U.S. Dept. Interior, Tech. Paper No. 58.

Saunders, G. W. 1972. The transformation of artificial detritus in lake water. Mem. Ist. Ital. Idrobiol. 29(Suppl.):261-288.

Schmitz, W. R., and A. D. Hasler. 1958. Artificially induced circulation of lakes by means of compressed air. Science 128:1088-1089.

Serns, S. L. 1976. Movement of rainbow trout across a metalimnion deficient in dissolved oxygen. Prog. Fish. Cult. 38:54.

Shapiro, J. 1973. Blue-green algae: Why they become dominant. Science 197:382-384.

Shapiro, J. 1979. The need for more biology in lake restoration. Proc. Natl. Conf. Lake Restoration. U.S. Environ. Prot. Agency.

Shapiro, J., and H. O. Pfannkuch. 1973. The Minneapolis chain of lakes. A study of urban drainage and its effects. Interim Rep. No. 9. Limnol. Res. Center, Univ. Minnesota.

Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: An ecosystem approach to lake restoration. In P. L. Brezonik and J. L. Fox, eds. Proc. Symp. on Water Quality Management through Biological Control. Univ. Florida and U.S. Environ. Prot. Agency, Gainesville. pp 85-95.

Shapiro, J., G. Zoto, and V. Lamarra. 1977. Experimental studies on changing algal populations from blue-greens to greens. Contrib. No. 168. Limnol. Res. Center, Univ. Minnesota.

Shilo, M. 1971. Biological agents which cause lysis of blue-green algae. Mitt. Internat. Verein. Limnol. 19:206-213.

Sikorowa, A. 1978. Changes of the distribution and number of the bottom fauna as an effect of artificial lake aeration. Verh. Internat. Verein. Limnol. 20:1000-1003.

Smith, S. A., D. R. Knauer, and T. L. Wirth. 1975. Aeration as a lake management technique. Wisconsin Dept. Natur. Resour., Tech. Bull. No. 87. 39 pp.

Steichen, J. M., J. E. Garton, and C. E. Rice. 1974. The effect of lake destratification on water quality parameters. Ann. Meeting of Amer. Soc. of Agric. Engineers.

Symons, J. M., W. H. Irwin, E. L. Robinson, and G. G. Robeck. 1967. Impoundment destratification for raw water quality control using either mechanical- or diffused-air pumping. J. Amer. Water Works Assoc. 59:1268-1291.

Symons, J. M., J. K. Carswell, and G. G. Robeck. 1970. Mixing of water supply reservoirs for quality control. J. Amer. Water Works Assoc. 62:322-334.

Teerink, J. R., and C. V. Martin. 1969. Artificial destratification in reservoirs of the California State Water Project. J. Amer. Water Works Assoc. 62:436-440.

Thomas, E. A. 1966. Der Pfaffikersee vor, wahrend, und nach kunstlicher Durchmisching [In German]. Verh. Internat. Verein. Limnol. 16:144-152.

Toetz, D. W. 1977a. Biological and water quality effects of whole lake mixing. Okl. Water Resour. Res. Inst. Final Tech. Rep. A-068-OKLA. 78 pp.

Toetz, D. 1977b. Effects of lake mixing with an axial flow pump on water chemistry and phytoplankton. Hydrobiologia 55:129-138.

Toetz, D. W. 1979. Biological and water quality effects of artificial mixing of Arbuckle Lake, Oklahoma, during 1977. Hydrobiologia 63:255-262.

Toetz, D., J. Wilhm, and R. Summerfelt. 1972. Biological effects of artificial destratification and aeration in lakes and reservoirs--Analysis and bibliography. Oklahoma Cooperative Fishery Unit Rept. No. REC-ERC-72-33.

Turner, H. J., R. E. Towne, and T. P. Frost. 1972. Control of algae by mixing. J. New Engl. Water Works Assoc. 86:267-275.

U.S. Environmental Protection Agency. 1976. Quality criteria for water. U.S. Gov. Print. Off., Washington, D.C. 256 p.

von Ende, C. N. 1979. Fish predation, interspecific predation, and the distribution of two Chaoborus species. Ecology 60:119-128.

Webster, K. E., and R. H. Peters. 1978. Some size-dependent inhibitions of large cladoceran filterers in filamentous suspensions. Limnol. Oceanogr. 23:1238-1245.

Weiss, C. M., and B. W. Breedlove. 1973. Water quality changes in an impoundment as a consequence of artificial destratification. N. Carolina Water Resour. Res. Inst., Rept. No. 80.

Whipple, W., Jr., J. V. Hunter, F. B. Trama, and T. J. Tuffey. 1975.

Oxidation of lake and impoundment hypolimnia. Water Resour. Res. Inst., Rutgers Univ. Final Rept. on Proj. No. B-050-N.J.

Wilhm, J., and N. McClintock. 1978. Dissolved oxygen concentration and diversity of benthic macroinvertebrates in an artificially destratified lake. Hydrobiologia 57:163-166.

Wirth, T. L., and R. C. Dunst. 1967. Limnological changes resulting from artificial destratification and aeration of an impoundment. Wisconsin Conserv. Dep., Fish. Res. Rep. No. 22.

Wirth, T. L., R. C. Dunst, P. D. Uttormark, and W. Hilsenhoff. 1970. Manipulation of reservoir waters for improved quality and fish population response. Wisc. Dep. Natur. Resour., Madison. Rep. No. 62. 23 pp.

Zaret, T. M., and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. 21:804-813.

CONTROL OF NON-POINT NUTRIENT CAUSED ALGAL PROBLEMS ESPECIALLY BY DILUTION

Eugene B. Welch
Department of Civil Engineering
University of Washington
Seattle, Washington 98195

ABSTRACT

Non-point sources of nutrients that lead to nuisance algae blooms can theoretically be controlled by prevention of excessive development in watersheds thus keeping phosphorus yields below critical limits for the lake in question. Treatment of runoff in wetland areas appears promising; however, there is little evidence to suggest that retention ponds are effective at removing phosphorus and nitrogen. Diversion of stormsewers has been proposed and implemented and should be effective if nutrient concentration in the inflow is high, thus being analogous to sewage effluent diversion. Dilution of non-point sources of nutrients has been successful in at least two situations and has shown enough promise in at least five other instances in the West to be proposed.

Lake quality in Moses and Green Lakes, Washington, improved by over 70 and 50 percent, respectively, in terms of chl*a*, total phosphorus and visibility. This occurred as a result of dilution rates on the order of 0.5 to 1.0 percent per day during the spring summer growth period--about ten times the normal rates. Dilution of allelopathic excretory products appears to have more merit as a cause for inhibition of blue-greens and favoring diatoms than does the decrease in nutrient content. If so, the addition of even relatively rich water could benefit lake quality.

INTRODUCTION

Non-point or diffuse sources that contribute nutrients to surface waters include runoff from residentially and commercially developed areas, leachate from septic tank drainfields, agricultural runoff and groundwater. Internal recycling of nutrients in lakes, largely from direct release from bottom sediments or via rooted macrophytes, may also be regarded as important non-point sources in certain instances. Although there may be variations in the fraction of phosphorus available (Schaffner and Oglesby, 1978, and Rast and Lee, 1978), inputs from point and non-point sources alike contribute to the total loading to the water body. Because total loading and resulting concentration of phosphorus, more than any other factor, determines the trophic state and algae bloom intensity of fresh water bodies, control of phosphorus will in most cases provide control of algae problems (Vollenweider, 1968, 1976; Dillon and Rigler, 1974, 1975; Larsen and Merceir, 1976; Chapra and Tarapehak, 1976).

Controls for non-point sources of phosphorus fall under one of primarily four categories--prevention, treatment, diversion or dilution. Prevention would entail controls on residential and commercial development in a watershed to maintain P yields to less than the rate predicted to cause problems. Treatment involves subjecting the runoff water to a process that effectively removes phosphorus. Diversion naturally necessitates another water body to receive the nutrient-rich runoff and associated transport facilities. Dilution entails the addition of water lower in phosphorus content to the water body, thus reducing the concentration available for algae production.

APPROACHES TO CONTROL

PREVENTION OF URBAN P YIELD

Although just beginning, the prevention of bloom problems in lakes through enforcement of development limitations may prove effective. Using the Vollenweider modelling approach, with sedimentation rates estimated from flushing (Larsen and Mercier, 1976), watershed yields of P can conceivably be limited to prevent an eutrophic state (Dillon and Rigler, 1975; Gilliom, 1980). The three main difficulties are: 1) because of an internal P source, the trophic state may not conform to the external loading model, 2) established P yields through runoff from different land use types are inappropriate for the areas in question, and 3) the nature and frequency of failure in septic tank drainfields is poorly known.

P yield from different land use types is variable, but the trend is usually the same; pasture exceeds forest, urban exceeds pasture and agriculture exceeds urban (Table 1). Within the urban type the yield can be related to dwelling density and precent of impervious surface (Buffo, 1979), with yields differing by several fold. As an example of how preventative measures may protect a lake, the development of the eastside of Lake Sammamish may be restricted in many areas to 0.5 dwellings ha^{-1} and in others to 2.5 ha^{-1}. The average on the eastside now is about 2.5 ha^{-1} and the calculated yield of P is 17 kg km^{-2} $year^{-1}$. On the more developed westside the dwelling density ranges from 2.5 to 75 ha^{-1} with an average of about 10 ha^{-1} and the P yield is estimated at 60 kg km^{-2} $year^{-1}$. With the westside extensively developed the steady state P content in the lake is predicted to be 22 $\mu g\ l^{-1}$, but if the eastside were equally developed P content would rise by 20 percent to 26 $\mu g\ l^{-1}$ (Table 2).

TABLE 1. Watershed yields of phosphorus in kg km^{-2} $year^{-1}$

Reference	Forest	Forest + Pasture	Agriculture	Urban
Omernick (1976)	8.3	18.4	31	30
Dillon and Kirschner (1975)	11.7	23.3		
Welch et al. (in press)		17		60
Hickock (1979)				40
Schaffner and Oglesby (1978)	11.7		46	

TABLE 2. EFFECT ON P LOADING TO LAKE SAMMAMISH OF DEVELOPING AN ADDITIONAL 26% OF THE WATERSHED TO AN AVERAGE OF 10 DWELLINGS HA^{-1}

	DEVELOPMENT	
	WESTSIDE 18% WATERSHED	WEST + EASTSIDE 44% WATERSHED
P YIELD, KG KM^{-2} YR^{-1}	50	60
P LOAD, MG M^{-2} YR^{-1}	684	819
P INFLOW, μG L^{-1}	69	83
P LAKE, μG L^{-1}	22	26
% INCREASE		20

TREATMENT OF STORMWATER

Reduction in non-point P loading from watersheds already developed has not been adequately demonstrated. The technique usually employed is retention ponds to curtail peak runoff and in so doing peaks in P loading are reduced. However, P is probably associated more with light colloidal matter and not with larger particles, the fraction that would mostly fall out in detention ponds. According to the model of Larsen and Mercier (1976), flushing rate would need to be lowered to 0.01 yr^{-1} in order to retain 90 percent of the P, although it is doubtful that their relationships would apply directly to stormwater settling basins. Nevertheless, it is likely that pond volume would need to be very large in most cases to effectively trap P, and as yet the effectiveness of such detention ponds has not been adequately demonstrated.

The most effective treatment scheme for urban stormwater might be acheived by directing it through wetlands. Although not thoroughly investigated some evidence suggests that retention efficiencies of P can approach 60-80 percent (Hickock, 1979; Murdock and Capobianco, 1979). The purchase of wetlands for that purpose is being increasingly considered by municipalities. Such wetland areas serve the dual purpose of water volume retention and minimized peak flows in receiving streams, similar to retention ponds.

DIVERSION OF STORMWATER

Diversion of stormwater should be theoretically as effective as sewage diversion in some instances where runoff water is highly concentrated with nutrients. Few instances exist where such a technique has been implemented. One exception is Mirror Lake, Wisconsin, where a point source of stormwater, which represented 50-60 percent of the total P load, was diverted to a nearby stream. However, no immediate improvement in the lake was observed in terms of P content, plankton productivity nor biomass of blue-green algae, all of which had been previously thought to be related to the stormwater P source (Knauer, 1975, and personal communication). As in the case of other lakes with internal sources, improvements may be evident after several years.

In a slightly different situation, diversion of three stormwater inputs to Lake Ballinger, Washington, was proposed as a restoration alternative. Although 31 percent of the lake's P load came from those inputs, diversion of the stormwater was projected to decrease the lake P content by only 5 percent (Table 3). The relatively negligible impact on Lake P content was due to the nearly proportional decrease in flushing rate that would have occurred with diversion. In other words, the P concentration in the inflow was not terribly high. Hypolimnetic withdrawal and dilution were seen as better alternatives in that case (Welch et al., 1977).

DILUTION

The technique of diluting inflow or lake non-point nutrients with water of lower nutrient concentration is often called dilution and/or flushing. Although flushing can control algae biomass through cell washout (Welch, 1979), the lake quality benefits in the two cases where data exist for evaluation resulted largely from dilution. This is because water exchange rates were deemed too low to afford a washout effect. Besides Green Lake and Moses Lake, four other lakes in Washington State are proposed or considered for dilution--Vancouver, Wapato, Sacajawia and Fenwick. Although "dilution" of lake water has been identified as an important or potentially important deterrent to algae abundance, particularly the nuisance blue-greens, in other lakes (Keating, 1978; Goldman, 1968; Findenegg, 1966), adequate data for a test case exist for only Green and Moses Lakes.

Green Lake, with a volume of $4.12 \times 10^6 m^3$, has been diluted with city water containing about $6 \mu g \ell^{-1}$ total P since 1965. During 1965-1967 when data are available for comparison

TABLE 3. RESTORATION TECHNIQUES FOR L. BALLINGER, WASH.

INITIAL ANNUAL MEAN $P = 37\ \mu g\ L^{-1}$

TREATMENT	EXPECTED P	% DECREASE
HYPOLIMNETIC WITHDRAWAL	32	14
DILUTION WITH CITY WATER ($10\ \mu g\ L^{-1}$ P)	18	51
DIVERSION OF STORMWATER (31% OF P LOAD)	35	5
DIVERSION OF STORMWATER PLUS HYPOLIMNETIC WITHDRAWAL	30	19

with the pre-dilution state (1959), the improvement in algae biomass (chl*a*), total P content and visibility (Secchi disk) was about 73 percent (Oglesby, 1969; Welch, 1979). The average water exchange (flushing) rate during this period was only 0.6 percent per day (2.6 yr^{-1}), not an unusually high rate. Two-thirds of the exchange rate was due to the addition of city water which has remained rather constant to the present.

Moses Lake represents the most extensive test case for dilution water addition as a control for non-point nutrient loading. The lake is large (2753 ha, $154X10^6m^3$) and most of it is unstratified and less than its 5.6m mean depth. The years when control data were compiled were relatively wet--the flushing rate at that time was about 2 yr^{-1}. The non-point nutrient load (2 and 19 $g\ m^{-2}\ yr^{-1}$ of P and N, respectively) came largely from agricultural irrigation flow. Chl*a*, total P and Secchi disk averaged 45 $\mu g\ l^{-1}$, 156 $\mu g\ l^{-1}$ and 0.9 m during the summers of 1969-70 and blue-green algae, largely *Aphanezomenon* and *Microcytis*, represented about 96 percent of the phytoplankton volume.

Moses Lake serves as one feed route for Columbia River water to Pot Holes Reservoir, the main storage impoundment for the Columbia Basin Irrigation Project. Thus, facilities existed for testing the effects of dilution water with the purpose of determining optimum patterns of water input to control nuisance algal blooms. Columbia River water is low in N and P relative to the normal flow which is largely enriched irrigation return flow (Table 4).

Water was added to Parker Horn via Rocky Coulee Wasteway during the spring-summer period of 1977, 78 and 79 (Figure 1). Although a variety of input patterns was desired for experimental purposes, little control was exerted over the amount and timing of water input. As Table 5 shows, three periods of dilution were provided in 1977 and 1979, but only one in 1978. The total number of days of dilution ranged from 60 to 138 and the average exchange rates

TABLE 4. INFLOW CONCENTRATIONS ($\mu g\ L^{-1}$) TO PARKER HORN DURING MAY-SEPTEMBER, 1977 AND 1978.

	TOTAL P	TOTAL N	PO_4-P	NO_3-N
CRAB CREEK	150	1402	46	862
INFLOW WITHOUT DILUTION	148	1331	90	1096
EASTLOW CANAL DILUTION WATER	25	308	8	19

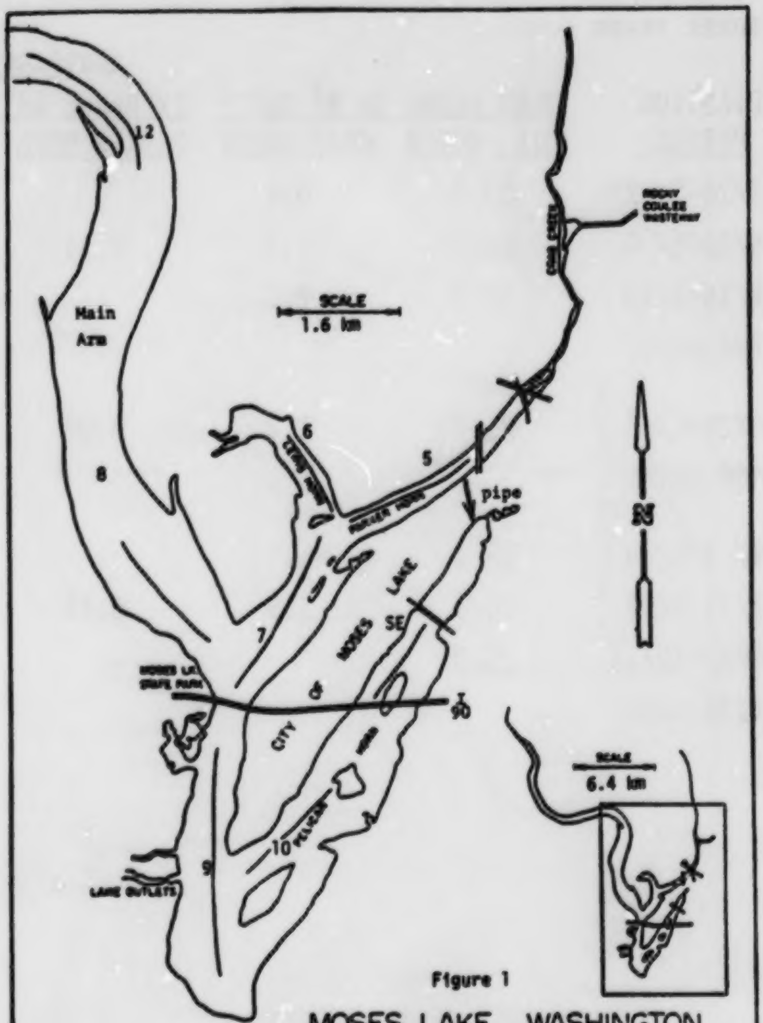

12
Main Arm
SCALE
1.6 km
ROCKY COULEE WASTEWAY
CRAB CREEK
6
5
PARKER HORN
pipe
8
LAKE
MOSES
SE
7
MOSES LK. STATE PARK
CITY
of
90
HORN
PELICAN
10
9
LAKE OUTLETS
SCALE
6.4 km

Figure 1

MOSES LAKE, WASHINGTON
Showing sampling transect locations and treated sewage effluent (SE) and pipe connecting Parker and Pelican Horns proposed in Phase II.

TABLE 5. DILUTION WATER INFLOW RATES TO PARKER HORN, MOSES LAKE VIA CRAB CREEK SHOWING HYPOTHETICAL WATER EXCHANGE RATES FOR PARKER HORN (8% VOLUME) AND THE WHOLE LAKE (100% VOLUME) DURING APRIL THROUGH SEPTEMBER OF THE THREE YEARS

	DILUTION	MEAN FLOWS IN M^3 SEC^{-1}		APRIL-SEPTEMBER EXCHANGE RATE IN $DAYS^{-1}$	
YEAR	PERIOD	DIL. WATER	CRAB CREEK	PARKER HORN	WHOLE LAKE
1977	3/20-5/ 7	33.6	0.4		
	5/22-6/ 4	10.5	1.3	0.11	0.009
	8/14-9/18	17.3	2.5		
	(96 DAYS)				
1978	4/20-6/18	21.7	1.7	0.07	0.006
	(60 DAYS)				
1979	4/ 3-6/ 4	25.1			
	7/11-8/28	16.3	1.5	0.13	0.010
	9/20-10/18	23.2			
	(138 DAYS)				

during April-September for Parker Horn, where the water enters (Fig. 1), ranged from 0.07 to 0.13 day^{-1}. The normal summer exchange is 0.01 day^{-1}. Note that for the whole lake the Parker Horn inflow (excluding groundwater and flow from Rocky Ford Creek into the main arm) represented an exchange rate of only 0.6 to 1.0 percent per day (Table 5)--quite comparable to that in Green Lake.

Improvement of lake quality in 1977-79, compared to 1969-70, was near or in excess of 50 percent for total P and N as well as chl*a* for not only Parker Horn but also most of the lake (Figs. 2 and 3). Visibility was also substantially improved. Of course, quality was better in Parker Horn where the fraction of dilution water was greater, but most of the lake responded almost as well. The reason was that, largely due to the wind and probably the large volumes introduced, the dilution water was effectively distributed throughout the lake (Welch and Patmont, in press).

Presentation of means for the May-September period obscures the high quality conditions, such as visibility reaching a maximum in most of the lake of 3 m in June as well as maximum chl*a* reaching peaks near 50 $\mu g\ l^{-1}$ in late July-August after water input had been curtailed for 2-4 weeks. Unless water was continually added, blooms would return as the fraction of dilution water left in the lake declined. This "boom and bust" situation promoted by large inputs followed by no input at all has prompted proposing continual input at low rates throughout the summer employing similar total amounts of water. The large quantities added over a short period of time that exchanged water in Parker Horn at the rate of about 20 percent per day and in most of the lake at 2-3 percent per day are considered unnecessary considering the nature of the effect of dilution water on the phytoplankton, particularly the blue-greens.

FIGURE 2. WATER QUALITY IMPROVEMENT IN PARKER HORN (8% VOLUME) FOLLOWING DILUTION WATER ADDITIONS IN 1977-1979. DATA REPRESENT MAY THROUGH SEPTEMBER MEANS FROM TRANSECT WATER COLLECTIONS AT 0.4 M DEPTH

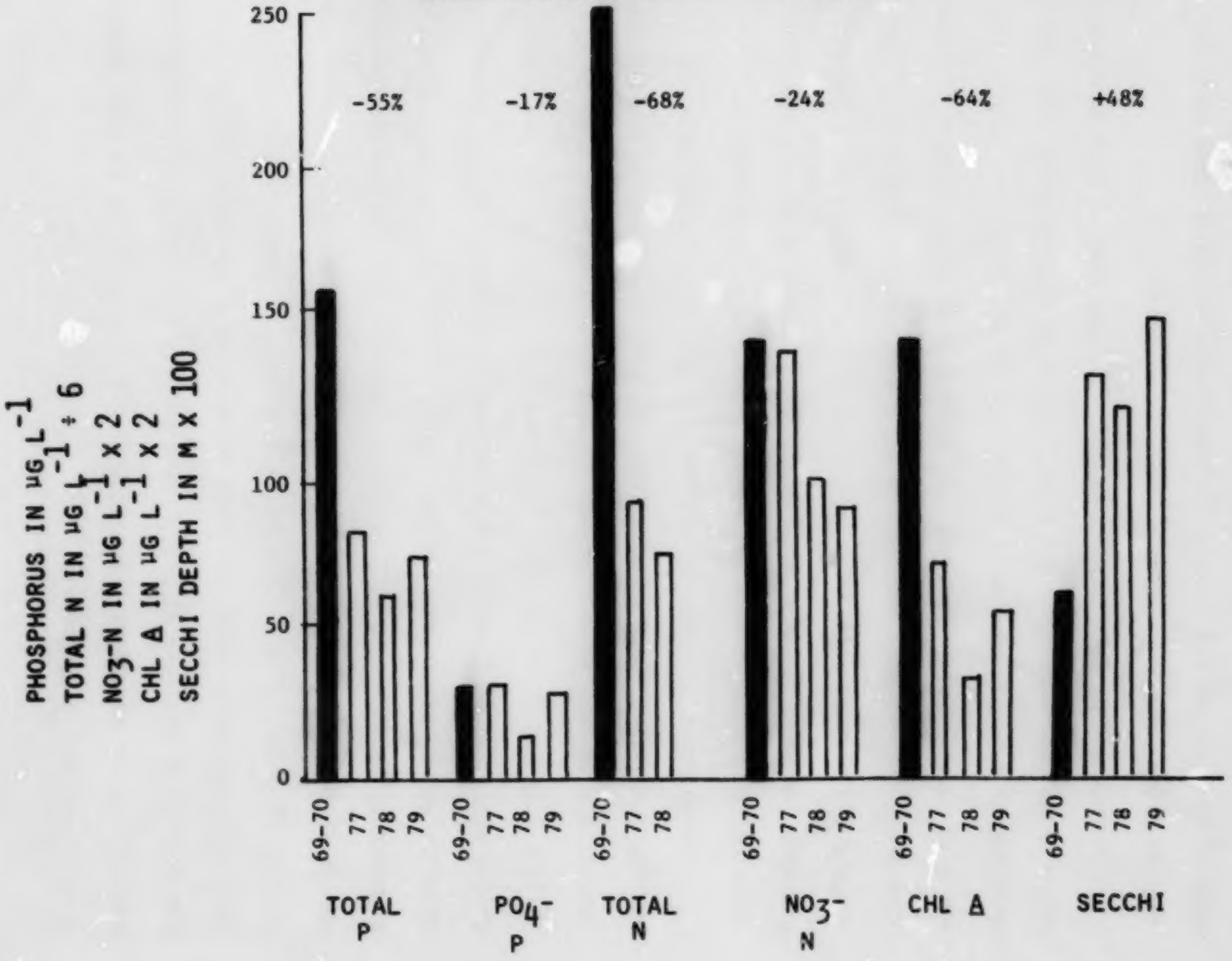
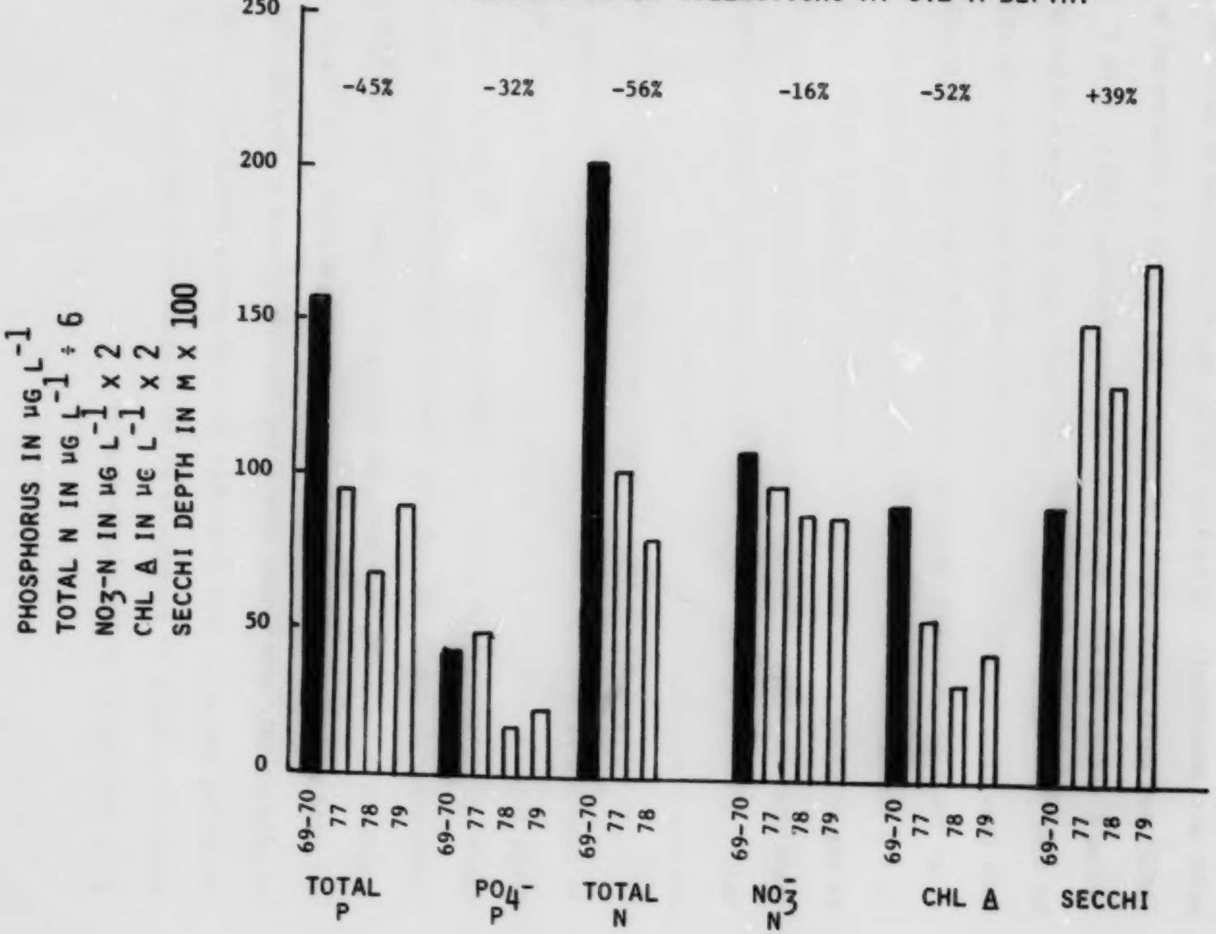


FIGURE 3. WATER QUALITY IMPROVEMENT IN MOSES LAKE (58% VOL.) FOLLOWING DILUTION WATER ADDITIONS IN 1977-1979. DATA REPRESENT MAY THROUGH SEPTEMBER MEANS FROM TRANSECT WATER COLLECTIONS AT 0.2 M DEPTH.



While the biomass of algae was reduced by over 50 percent, relative to pre-dilution years, the fraction comprising blue-greens also decreased markedly to 68 percent (see Welch and Patmont, in press, counting and other analytical procedures). Inhibition of blue-green growth by dilution water was demonstrated by Buckley (1971) and is discussed by Welch et al. (1972) and Welch and Patmont (in press). The effect is illustrated in Tables 6 and 7, the data for which came from Buckley (1971). Here it can be seen that for the first in situ experiment both blue-green algae and diatoms grew best in full lake water and their growth declined as the dilution water fraction increased, although blue-greens did more poorly than diatoms. In the second experiment (Table 7) blue-greens again did increasingly poorer as the dilution water fraction increased, but in contrast to the first experiment diatoms actually improved in growth with more dilution water. Certainly dilution water inhibits blue-greens more than diatoms and sometimes diatoms even prefer straight dilution water.

One explanation of this is that blue-greens become abundant in Moses Lake in June and as their populations increase the allelopathic excretory products tend to favor their own growth and inhibit that of diatoms. Diatoms may have preferred lake water to dilution water in the early (June) experiment prior to the buildup of allelopathic substances but later on (July) the substance buildup may have been inhibitory to diatoms. The addition of dilution water to the lake could be providing a similar effect--a dilution of allelopathic substances permitting improved growth of diatoms while rendering the water less favorable for blue-greens themselves. Surely the improved response of diatoms to dilution water would not support the cause as a toxic agent in the dilution water.

TABLE 6. MAXIMUM GROWTH RATE OVER THE FIRST FOUR TO SIX DAYS OF A TWO-WEEK IN SITU EXPERIMENT, CONDUCTED JUNE 15-27, 1970, ON THE EFFECT OF COLUMBIA RIVER DILUTION WATER ON BLUEGREEN ALGAE AND DIATOMS IN MOSES LAKE, WASHINGTON. AMBIENT LAKE CONCENTRATIONS OF BLUEGREENS AND DIATOMS WERE 2000 ML^{-1} AND 33 ML^{-1}, RESPECTIVELY

WATER COMPOSITION	BLUEGREENS		DIATOMS	
LAKE/DILUTION	μ, DAY^{-1}	NO. ML^{-1}	μ, DAY^{-1}	NO. ML^{-1}
100/ 0	0.31	1677	0.83	2768
50/ 50	0.12	686	0.54	3589
0/100	-1.15	22	0.41	616

TABLE 7. MAXIMUM GROWTH RATE OVER THE FIRST FOUR TO SIX DAYS OF A TWO-WEEK IN SITU EXPERIMENT, CONDUCTED JULY 8-23, 1970 ON THE EFFECT OF COLUMBIA RIVER DILUTION WATER ON BLUE-GREEN ALGAE AND DIATOMS IN MOSES LAKE, WASHINGTON. AMBIENT LAKE CONCENTRATIONS OF BLUEGREENS AND DIATOMS WERE 3174 ML^{-1} AND 2 ML^{-1}, RESPECTIVELY.

WATER COMPOSITION	BLUEGREENS		DIATOMS	
LAKE/DILUTION	μ, DAY^{-1}	MEAN NO. ML^{-1}	μ, DAY^{-1}	MEAN NO. ML^{-1}
100/ 0	0.28	6817	0.08	182
75/ 25	0.31	4808	0.09	184
50/ 50	0.23	3354	0.20	246
25/ 75	0.06	989	0.37	636
0/100	-0.35	156	0.81	1573

Keating (1978) has suggested, with supporting observations and experiments, that dilution of allelopathic substances accounts for much of the natural successional pattern of phytoplankton (blue-greens and diatoms). Other examples exist where diatoms flourish in enriched lakes even in summer and blue-greens seldom cause blooms. Blue-greens are of minimal significance in Tennessee Valley impoundments even though they receive high loading rates of P (Table 8) and sustain rather high rates of productivity (nearly 1500 mg C m^{-2} day^{-1} in Wheeler during summer). The reason may well be the relatively rapid summer exchange rates. Thus, "dilution" with even high nutrient water may provide benefits of controlling blue-green blooms.

Although nitrogen reaches very low levels in Moses Lake and no doubt limits growth rate at times, it is not likely that the reduction in algal biomass resulted from reductions in total nutrient concentrations. Actually, chl_a_ was reduced to one-half the level that should have been afforded by the reduction of total P as predicted from the equation of Dillon and Rigler (1974), assuming P to be limiting and biomass was equilibrated with available nutrients. As far as NO_3^- is concerned, lower levels were actually observed in 1969-70 than in 1977-79, no doubt simply because algal crops were greater in 1969-70 and soluble nutrient concentrations are usually inversely correlated with biomass. Given the small and inconsistent changes in soluble nutrient fractions (Figs. 2 and 3) with dilution and the fact that populations could be observed to increase at respectable rates even though NO_3-N and PO_4-P were rather low, the improvement in lake quality (reduction in algal biomass) is not thought to have been caused by nutrient limitation afforded by the low levels of N and P in dilution water. Free CO_2 increased on the average by about two-fold following dilution (23 versus 45 $\mu g\ l^{-1}$) and may have influenced species succession. These possibilities have been discussed elsewhere (Welch and Patmont, in press).

TABLE 8. ANNUAL PHOSPHORUS LOAD, MEAN CONCENTRATION AND FLUSHING RATE (ρ) AND SUMMER VALUES FOR CHL A AND SECCHI VISIBILITY (SD) IN 18 TVA RESERVOIRS (B.G. ISAM, TVA, PERSONAL COMMUNICATION).

	9 MAINSTEM	9 STORAGE	WHEELER
G P M^{-2} YR^{-1}	19.8	3.58	8.4
P, μG L^{-L}	46	51	
ρ, YR^{-1}	37	2.4	39
CHL A μG L^{-L}	5.5	6.7	3.3*
SD, M	1.0	2.2	

*PHYTOPLANKTON COMPOSED OF < 5% BLUEGREENS

For the optimum control of nuisance algal blooms in Moses Lake the primary consideration is to exchange the lake water with Columbia River water to a level of near 50 percent and maintain that level over most of the summer. That can be accomplished in more than one-half the lake with a dilution water input of 6 $m^3 sec^{-1}$, which would provide a dilution water-to-Crab Creek flow ratio of 3:1. Crab Creek water is essentially lake water before nutrients are processed and excretory products accumulate. Therefore, the 3:1 ratio should easily insure that at equilibrium 50 percent of the lake water is of Columbia River origin. That ratio provides a safety factor for the ground water contribution, although it is not a large contributor of P. At that constant inflow rate Parker Horn would be exchanged (flushed) at 5 percent per day (0.05 day^{-1}), the whole (100%) lake at 0.4 percent per day (0.004 day^{-1}) and 58 percent of the lake at 0.7 percent per day-- the same rate as in Green Lake. That would be on the order of ten times the normal exchange rate during summer.

RESEARCH NEEDS

From the standpoint of prevention and control of non-point source nutrients, improvements in on-site wastewater treatment (i.e., septic tanks) should be sought. Improvements in their effectiveness in poor soil, high rainfall areas as well as placement and continued management are needed. Improved techniques of defining nutrient yields from different land use types and relating these yields to lake response is needed.

The mechanism(s) for blue-green inhibition in lakes with rather high summer rates of dilution/flushing should be determined. If blue-green inhibition can be achieved with even high-nutrient water, the technique of dilution/flushing would have broader appeal. Further, the addition of polymers should be tested to control blue-green excretory products and favor the dominance of other algae.

REFERENCES

Buckley, J.A. 1971. Effects of low nutrient dilution water and mixing on the growth of nuisance algae. M.S. thesis, Univ. of Washington, Seattle.

Buffo, J. 1979. Water pollution control early warning system: section 1, non-point source loading estimates. Municipality of Metro Seattle Report, 47 pp.

Chapra, S.C. and S.J. Tarapehak. 1976. A chlorophyll *a* model and its relationship to phosphorus loading plots in lakes. *Water Resources Res*. 12:1260-1264.

Dillon, P.J. and F.G. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. *Limnol. and Oceanogr*. 19:767-773.

Dillon, P.J. and W.B. Kirschner. 1975. The effects of geology and land use on the export of phosphorus from watersheds. *Water Res*. 9:135-148.

Dillon, P.J. and F.G. Rigler. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. *Jour. Fish Res. Bd. Canada* 32:1519-1531.

Findenegg, I. 1966. Relationship between standing crop and primary productivity. *In* C.R. Goldman, Primary Productivity in Aquatic Environments. Proceedings *of* an IBPPF Symposium, pp. 271-290.

Gilliom, R. 1980. Estimation of background loadings and concentrations of phosphorus for lakes in the Puget Sound Region, Washington. U.S. Geological Survey, Open File Report, OF 80-328, 37 pp.

Goldman, C.R. 1968. Limnological aspects of Clear Lake, California with special reference to the proposed diversion of Eel River water through the lake. Report to Fed. Water Poll. Cont. Admin.

Hickock, E.A. 1979. Wetlands and organic soils for the control of urban stormwater. *In* Lake Restoration, Proceedings of a Conference, EPA-400/5-79-001, pp. 153-160.

Keating, K.I. 1978. Blue-green algal inhibition of diatom growth: transition from mesotrophic to eutrophic community structure. *Science* 199:971-973

Knauer, D.R. 1975. The effect of urban runoff on phytoplankton ecology. *Vert. Internat. Verein Limnol*. 19:893-903.

Larsen, D.P. and H.T. Mercier. 1976. Phosphorus retention capacity of lakes. *J. Fish. Res. Bd. Canada* 33;1742-1750.

Murdock, A. and J.A. Capobianco. 1979. Effects of treated effluent on a natural marsh. *J. Water Poll. Cont. Fed*. 51:2243-2256.

Oglesby, R.T. 1969. Effects of controlled nutrient dilution on the eutrophication of a lake. *In* Eutrophication: causes, consequences and correctives, National Academy *of* Sci., Washington, D.C. p. 483-493.

Omernick, J.M. 1976. The influence of land use on stream nutrient levels. Ecol. Res. Series, EPA-600/3-76-014.

Rast, W. and G.F. Lee. 1978. Summary analysis of the North American (U.S. Portion) OECD eutrophication project: nutrient loading - lake response relationships and trophic state indices. Ecol. Res. Series (EPA-600/3-78-008.

Schaffner, W.R. and R.T. Oglesby. 1978. Phosphorus loadings to lakes and some of their responses. Part I. A new calculation of phosphorus loading and its application to 13 New York lakes. Limnol. and Oceanogr. 23:120-134.

Vollenweider, R.A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Tech. Report DAS/CSI/68.27. Organization for Economic Cooperation and Development (OECD), Paris, 250 pp.

Vollenweider, R.A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. 33:53-83.

Welch, E.B., J.A. Buckley and R.M. Bush. 1972. Dilution as an algal bloom control. J. Water Poll. Cont. Fed. 44:2245-2265.

Welch, E.B., D.N. Given and C.J. Neel. 1977. Water quality problems and alternatives for the restoration of Lake Ballinger. Part II. The lake. Municipality of Metro Seattle Report, pp. 63-120.

Welch, E.B. 1979. Lake restoration by dilution. In Lake Restoration, Proceedings of a National Conference, U.S. Environ. Protec. Agency, EPA 400/5-79-001, pp. 133-139.

Welch, E.B. and C.R. Patmont. Lake restoration by dilution; Moses Lake, Washington. Water Research, in press

Welch, E.B., C.A. Rock, R.C. Howe and M.A. Perkins. Lake Sammamish response to wastewater diversion and increasing urban runoff. Water Research, in press.

LIMITS TO THE CONTROL OF ALGAL POPULATIONS BY GRAZING ZOOPLANKTON: THE ENVIRONMENTAL THEATER AND THE ECOLOGICAL PLAY*

Karen G. Porter
Department of Zoology and Institute of Ecology
University of Georgia
Athens, Georgia 30602

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In answer to the question, can grazers control algal abundance, I'd have to say well, maybe. It depends on the grazers, the algae, and the definition of the term "control." If you are interested in having grazers reduce algal abundance in order to improve water clarity and, in addition, to provide food for desirable, higher trophic levels, e.g. planktivorous game and forage fish, then the answer becomes easier to give. Of the potential grazers listed in Table 1, I'll consider the macrozooplankton, primarily the large crustaceans, as the grazers that both crop algae at high rates and are most heavily fed upon by fish. In a previous review (Porter, 1977), I summarized the gross differences in feeding behavior and ecology of the cladocera and the cyclopoid and calanoid copepods. Recent research (Porter and Orcutt, 1980; Porter, Orcutt, and Gerritsen, in

Table 1. Grazers feeding on planktonic algae

I. Macrozooplankton
    A. Cladocera
        1. large (*Daphnia*)
        2. small (*Ceriodaphnia*, *Bosmina*)
    B. Copepods
        1. cyclopoid
        2. calanoid
II. Microzooplankton
    A. rotifers
    B. protozoans
III. Vertebrate Herbivores
    A. Tadpoles
    B. Gizzard shad
    C. *Tilapia*
    D. Flamingoes

Table 2. Growth rates and life history (fitness) parameters of the large cladoceran, *Daphnia parvula*, and the small cladoceran, *Ceriodaphnia reticulata*, isolated from a Georgia lake and fed no food, the <1 μm filtered fraction of lake water, whole lake water containing 10^3 to 10^4 natural algal cells^{-1} and lake water enriched with 10^4 cells cc^{-1} of axenic *Chlamydomonas reinhardi*. (M. Pace and Y. Feig, unpublished data). Data were obtained with procedures similar to those of Porter and Orcutt (1980). Experiments were performed during May and June, 1980.

Treatments	% Growth	Ro Net Reproduction (♀/♀/generation)	r instantaneous rate of increase
Daphnia parvula			
particle free	3.16	-†	-
<1 μm fraction	35.58	0.39	-0.05
whole lake water	131.18	25.05	0.18
lake water + *Chlamydomonas*	198.37	66.55	0.24
Ceriodaphnia reticulata			
particle free water	-✝	-	-
<1 μm fraction	45.94	8.67	0.23
whole lake water	81.58	55.64	0.33
lakewater + *Chlamydomonas*	86.10	43.51	0.44

† no reproduction

✝ data not available

prep.) supports the generalizations made in that review that cladocerans, such as Daphnia, are primarily nonselective feeders; particle capture is directly related to (1) abundance and, therefore, encounter of the particles and (2) the efficiency with which the filtering mechanism captures and retains the particles. Daphnia can begin to grow and reproduce parthenogenetically when natural (Table 2) and laboratory (Porter and Orcutt, 1980) algae concentrations are between 10^3 and 10^4 cells cc^{-1}. Daphnia can feed on large particles such as 200 μm protozoans (Porter, Pace, and Battey, 1979) and <1 μm bacteria, but with reduced handling efficiencies, e.g. capture rate is lower than encounter rate (Figure 1). This reduced handling efficiency of very large and very small particles results in reduced ingestion rates and reduced growth and reproduction. This is evidenced by life table parameters of Daphnia parvula fed the <1 μm filtered fraction of natural lake water as compared with whole or algae enriched lake water (Table 2). However, the smaller cladoceran Ceriodaphnia reticulata is able to meet 50% of its requirements for growth and reproduction on the <1 μm fine particle fraction. This indicates that cladoceran body size is related to handling efficiencies of particles at the lower end of the particle spectrum as well as at the upper end (Burns, 1968). This, in turn, determines the relative abilities of cladoceran species to capture and utilize fine particles as food resources for growth and reproduction. This is an alternative (or additional) hypothesis explaining the succession from large to small cladocerans as eutrophication progresses (see Webster and Peters,1979 for others).

The major form of selection by cladocerans, if you wish to call it that, is rejection. Rejective feeding occurs when Daphnia filtering appendages become clogged at high food concentrations ($>10^4$ cells cc^{-1}) or

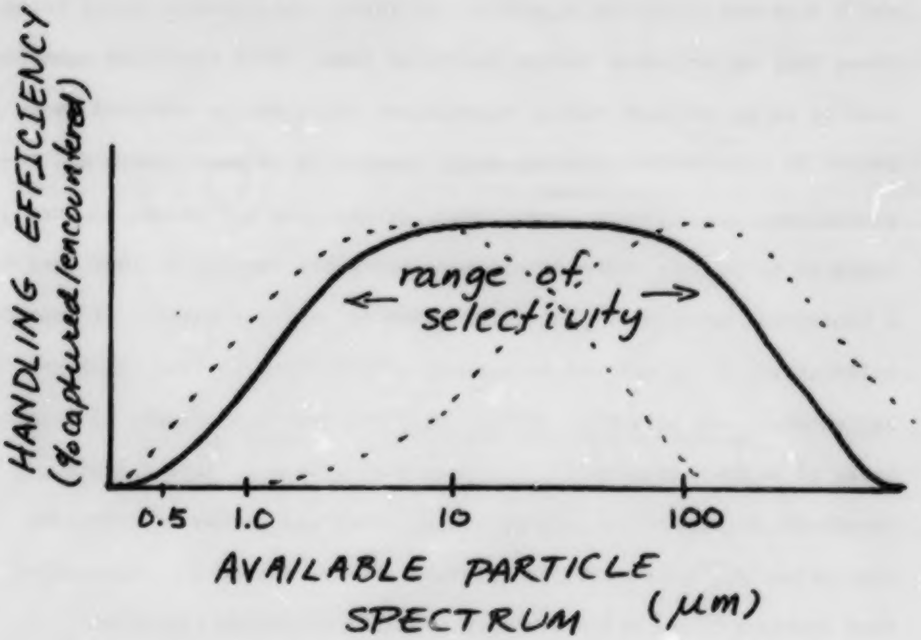

Figure 1. The handling efficiency of filter feeders is reduced at the upper and lower ends of the particle spectrum. Some groups such as the copepods show a high degree of flexibility and can alter their particle capture abilities by selective feeding behaviors. This is shown hypothetically by the dotted lines. Other filter feeders such as Daphnia have limited abilities to alter the efficiency with which particles are captured by them.

when they encounter large particles such as filamentous blue-greens, which clog the filtering apparatus, or filter unpalatable, toxic forms. These they reject after having collected them. This rejective behavior results in an enormous energy expenditure which can be measured as an increase in respiration rate and which results in reduced growth and reproduction, i.e. fitness (see Porter, Orcutt, and Gerritsen, in prep.). Compared to Daphnia copepods are more selective feeders in that they have a behavioral repertoire that allows them to employ a variety of appendage orientations to select and reject while continuing to feed (Alcaraz, Paffenhöfer, and Strickler 1980). They can feed selectively by tracking peaks of maximum abundance. Copepods also appear to have a feeding threshold, extensive high-energy stores which allow them to withstand starvation (and presumably to tolerate patchy, sparce and fluctuating food resources) and well-developed predator avoidance abilities.

I can tentatively generalize that the morphology, feeding behavior, and life history patterns of large cladocerans allow them to feed, grow, and reproduce best when algal food is abundant, digestible and of high nutritive quality for them. They are the ideal grazers in that they have high filtering rates and serve as favored food sources for fish. Copepods feed and reproduce at lower rates but appear to be more flexible and tolerant in their feeding behavior. These behavioral and life history differences can begin to explain the reduction in the Daphnia:copepod ratio seen during early stages of eutrophication. (The trend was originally described as a cladoceran:copepod shift by McNaught but should be clarified because small cladocerans increase while large ones decrease in relative abundance, see Webster and Peters, 1979). As eutrophication proceeds, there is often an increase in microbial and detrital production.

This favors the smaller cladocerans such as Ceriodaphnia which can feed more efficiently on them and eventually promotes the growth of microzooplankton such as rotifers and protozoans (Pace and Orcutt, in press). There is some anecdotal evidence for these forms feeding on large algal blooms but basically they represent a reduction in the body size of the zooplankton community with a concomitant reduction in its access to large and intermediate sized algae and its potential to control them. Environmental toxins and reduced oxygen tensions which reduce grazer abundances also reduce their control potentials.

In conclusion, grazers can control algae, to a point. If the algae are palatable and within the manageable size range and if community grazing rates are equal to or greater than doubling times of the cells, then algal populations cannot increase. Grazers cannot immediately control run-away algal blooms promoted by rapidly improved conditions for growth. Nor can they reduce large, unmanageable, or noxious forms by cropping. Selective grazing can shift the relative abundance among algal species in a community. This has been shown in a number of in situ manipulation studies. However, the composition of the algal community is eventually determined by the physical and chemical regime in a body of water. Within limits grazers can determine algal abundance and community composition, but ultimately, environmental conditions set the stage for biological interactions. There are numerous case studies and experiments which document the effect of the major nutrients phosphorus and nitrogen in promoting algal blooms, especially those of blue-green algae. Examples of control from high levels of the food chain (predatory fish and grazers) are harder to come by as J. Shapiro and I have shown. This should tell us which is an overriding influence.

If grazers are presented with an algal flora that is suitable in that it is in the manageable size range, digestible, palatable, and of high nutritional quality, then they should be able to limit its population growth, although not eliminate it. Increased production of edible forms should eventually be cropped to a level at which the grazers can no longer grow and reproduce. This is under 10^4 algal cells cc^{-1}, an acceptable level for water clarity purposes. However, eutrophication usually occurs by the differential enrichment of aquatic systems, which favors the bloom of large and filamentous algal forms and the enhancement of microbial and detrital production. Mild cases can produce the well-known Daphnia-copepod shift. Simple filter feeders such as Daphnia are inhibited by the filaments while the smaller cladocerans which can avoid them and the more flexible copepods which can more easily select among particles will increase. Intense eutrophication can result in an elimination of the larger grazers and the promotion of smaller microzooplankton (rotifers and protozoans) which can utilize the finer particulate matter. Eutrophication therefore shifts the particle spectrum from one which favors large herbivorous crustacean zooplankton to one which favors smaller microbial feeding microzooplankton. This, in turn, shifts the planktonic food web from a phytoplankton-large zooplankton base, available to desirable higher trophic levels, to a more microbial-detrital microzooplankton system.

If the goal is to promote a phytoplankton-zooplankton based aquatic food chain, then size distribution and the composition of the algal flora must be managed to be suitable for crustacean grazers such as Daphnia. We are then back to the initial problem of controlling nutrient availability to avoid an imbalance of inorganic macronutrients, such as phosphorus, which favor filamentous blue-greens and organic enrichments which favor microbial production.

In manipulating and controlling natural systems we are constantly faced with problems of stability. Stressing an ecosystem through enrichment ultimately results in a "switching" of the system to a new association of organisms. There are often multiple stable points to which a system can switch. The problem is maintaining the system at a desirable one.

Future research which will allow us to better manage algal-zooplankton systems includes:

1. Examining the available food particle spectrum, especially the size fraction under 1 μm in a variety of water types.
2. Examining the role of bacteria and detritus in aquatic food chains.
3. Including microzooplankton in analyses of planktonic community structure.
4. Determining the local and regional variability in algal-zooplankton interactions in order to better define algal food quality.
5. Developing an on-the-spot method for determining grazing potential on the available particle spectrum.

You will notice that I avoided listing algal species as good or poor quality food sources. This is because zooplankton species differ in their absolute abilities to utilize algae and because factors such as relative and absolute abundance (encounter probability), manageability (size and shape), toxicity, palatability, and nutritional quality of algal species may change over time, space, and in the eyes of their beholders.

REFERENCES

Alcaraz, M., G.A. Paffenhöfer, and J.R. Strickler. 1980. Catching the algae. in C.W. Kerfoot (ed.) A.S.L.O. Special Symp. III. The Evolution and Ecology of Zooplankton Communities. University Press of New England. Hanover, N.H.

Burns, C.W. 1968. The relationship between body size of filter-feeding cladoceran and the maximum size of particle ingested. Limnol. Oceanogr. 13:675-678.

Porter, K.G. 1977. The plant-animal interface in freshwater ecosystems. Am. Scientist 65:159-170.

Porter, K.G., M.L. Pace, and J.F. Battey. 1979. Ciliate protozoans as links in freshwater planktonic food chains. Nature 277:563-565.

Porter, K.G. and J.W. Orcutt. 1980. Nutritional adequacy, manageability, and toxicity as factors that determine the food quality of green and blue-green algae for Daphnia. in C.W. Kerfoot (ed.) A.S.L.O. Special Symp. III: The Evolution and Ecology of Zooplankton Communities, University Press of New England. Hanover, N.H.

Porter, K.G., J.D. Orcutt, and J. Gerritsen. In prep. Foraging behavior, energy allocation, and life history patterns of a generalist filter feeder: Daphnia (Cladocera: crustacea).

Webster, K. and R.H. Peters. 1979. Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspension. Limnol. Oceanogr. 23:1238-1245.

ALGAL CONTROL THROUGH TROPHIC-LEVEL INTERACTIONS: A SUBTROPICAL PERSPECTIVE

Thomas L. Crisman

Department of Environmental
Engineering Sciences

University of Florida
Gainesville, Florida 32611

ABSTRACT

Numerous investigators have proposed that the composition and abundance of algal populations can be controlled biologically through a manipulation of the community structure of phytoplankton consumers such as macrozooplankton, but the feasibility of this approach has not been evaluated for subtropical systems. Grazer communities in temperate lakes are rather simplistic with zooplankton such as large species of Daphnia exerting a major control over phytoplankton. Subtropical systems are more complex due to the absence of large daphnids and the domination of fish faunas in eutrophic lakes by phytophagous taxa including shad. It is suggested that management schemes for the biological control of phytoplankton consider regional differences in both the structure of grazer communities and the major "nuisance" phytoplankton species. Construction of regional rather than a national management scheme for the biological control of algae should be stressed.

INTRODUCTION

Natural or cultural eutrophication of aquatic systems is manifested as the increased production of either macrophytes or algae, especially blue-greens. It is generally accepted that such an enhancement of autotrophic production is directly proportional to the availability of some limiting nutrient, usually phosphorus (Vollenweider 1968, Dillon and Rigler 1974). Thus, the eutrophication of a lake basin can be stopped, if not reversed, by controlling point-source and nonpoint-source nutrient inputs to the system coupled with a reduction in nutrient cycling from lacustrine sediments.

Point-source inputs are the easiest nutrient source to control and may be achieved through efficient wastewater treatment and the modification of products such as detergents, but nonpoint influxes and internal nutrient cycling are often difficult to control. Of the recently advanced physical and chemical techniques for controlling the in-lake availability of nutrients for algal growth (Dunst et al. 1974), hypolimnetic and total water-column aeration (Fast 1979), nutrient inactivation (Cooke et al. 1978), and dilution (Welch 1979) show the greatest promise.

Biological control of the abundance and/or composition of algal populations is a viable alternative for lake restoration where either the cost or feasibility of reducing nutrient availability is excessive or the lag time between nutrient abatement and establishment of a desired algal community is too long. Bacteria (Burnham 1975, Daft and Stewart 1971) and cyanoviruses (Safferman and Morris 1964) have been demonstrated to be effective at controlling blue-green algal populations in the laboratory, but whole-lake manipulative experiments have not been attempted. The greatest potential for biological control of the composition and abundance of phytoplankton, at least in the near future, is through a detailed understanding of the role of zooplankton and fish as nutrient cyclers and algal grazers in freshwater systems. Before a comprehensive management plan is formulated for the biocontrol of algal populations, regional differences in trophic-level interactions must be delineated.

TROPHIC-LEVEL INTERACTIONS IN TEMPERATE LAKES

Filter-feeding zooplankton are the most important algal grazers in temperature systems. Haney (1971 and 1973) in a series of detailed in situ grazing experiments in Ontario lakes calculated that grazing zooplankton during periods of peak abundance (late spring and summer) filtered the entire water volume of his eutrophic and oligotrophic lakes, respectively, 4.69 and 1.14 times daily. It must be pointed out that the filtering rate of the total zooplankton community is a reflection of the abundance, composition, and mean body size of the zooplankton community; thus the impact of herbivory in temperate systems displays pronounced seasonal and trophic state variations.

Brooks and Dodson (1965) advanced the size efficiency hypothesis to explain the competitive interactions of large and small zooplankton for food (algae). It was suggested that whereas small zooplankton feed exclusively on small algae (nannoplankton), large zooplankton are both capable of feeding on larger algal forms (net plankton) beyond the size range grazed by small zooplankton and are more efficient at grazing nannoplankton than are small zooplankton. Thus, they postulated that in absence of intense vertebrate predation, large zooplankton would exhibit a competitive advantage over small zooplankton.

Macrozooplankton (cladocerans and copepods) dominate the zooplankton assemblages of oligotrophic and mesotrophic temperate lakes but are replaced by smaller-bodied macrozooplankton and microzooplankton in eutrophic systems. Within the cladocera, elimination of large daphnids and the replacement of *Bosmina coregoni* by the smaller *Bosmina longirostris* often accompanies the cultural eutrophication of temperate systems (Beeton 1969 and Kerfoot 1974). The general reduction in the body size of cladocerans with increasing eutrophication has been attributed to a pronounced reduction in the habitat of piscivorous fishes as a result of hypolimnetic de-oxygenation thus decreasing predation pressure on planktivorous fish species, the major size-selective vertebrate predators on zooplankton.

Given the fact that macrozooplankton are more efficient grazers than microzooplankton on all sizes of algae but are of reduced importance in eutrophic systems, the question remains whether macrozooplankton could successfully control algal populations in eutrophic systems if their population could be enhanced through the selective management of planktivorous fish populations. Population enhancement of large *Daphnia* species following elimination of planktivorous fishes has resulted in dramatic reductions in the algal biomass of several lakes in North America (Schindler and Comita 1972, Shapiro 1979a and 1979b) and Europe (Hrbacek *et al*. 1961, Hrbacek 1964, Shapiro 1979a and 1979b). Perhaps fortuitously, pronounced algal changes were associated with an increase of large *Daphnia* thus lending credence to the contention of Haney (1973) that, although large zooplankton in general are more efficient algal grazers than small zooplankton, large cladocerans are much more important grazers in temperate lakes than are copepods.

Thus, the greatest potential for biologically controlling algal biomass in temperate lakes is through a population enhancement of large zooplankters, especially *Daphnia*. As suggested by Shapiro (1979a, 1979b), the phytoplankton response to grazing by large zooplankters is not uni-directional but depends on the community structure and species composition of the initial algal assemblage. For example, increased daphnid populations resulted in a shift in algal dominance from blue-greens to greens, chrysophytes, diatoms, and euglenophytes in Severson Lake (Schindler and Comita 1972) and Wirth Lake, Minnesota (Shapiro 1979a), but the appearance of similar daphnid populations in Lake Washington (Shapiro 1979b), Clear Lake, California (Cook and Connors 1963) and experimental ponds in Minnesota (Lynch 1979) encouraged blue-green populations, especially *Aphanizomenon*. This seemingly unpredictable phytoplankton response is strongly controlled by the palatability and digestibility of individual algal species (Porter 1973, 1975, 1977; and Webster and Peters 1978) and the possible biochemically induced formation of large colonies unsuitable for zooplankton grazing such as observed for *Aphanizomenon* in the presence of large *Daphnia* (Hrbacek 1964, Shapiro 1979a and b). Thus, while the mechanism for biologically controlling algal populations in temperate lakes has been elucidated, the complex response of phytoplankton to an alteration of trophic-level interactions is poorly known.

TROPHIC-LEVEL INTERACTIONS IN SUBTROPICAL LAKES

ZOOPLANKTON. The most obvious difference in the zooplankton composition between temperate and subtropical Florida lakes is the absence of large daphnids in the latter systems. Large (*D. catawba*, *D. galeata mendotae*, *D. pulex*), intermediate (*D. laevis*), and small (*D. ambigua*), species of *Daphnia* have been reported from Georgia, but only the small-bodied *D. ambigua* has been encountered in any Florida lake. As a majority of the arguments regarding the importance of zooplankton as algal grazers in temperate systems have stressed the role of large *Daphnia* species, the question arises as to whether *Daphnia* is a significant controlling factor for algal populations in subtropical lakes.

Not only are the body sizes of macrozooplankton such as *Daphnia* reduced in all Florida lakes, but the importance of microzooplankton (ciliated protozoans and rotifers) is positively correlated with increasing trophic state (Bays *et al*. in preparation). The midsummer abundance of cladocerans and copepods displays only minor variation with trophic state, whereas the importance of rotifers greatly increases in eutrophic and hypereutrophic systems (Figure 1). In addition, Beaver *et al*. (1980) demonstrated that mean annual populations of ciliated protozoans in Florida lakes were highly correlated (r = 0.95) with increasing trophic state (Figure 2).

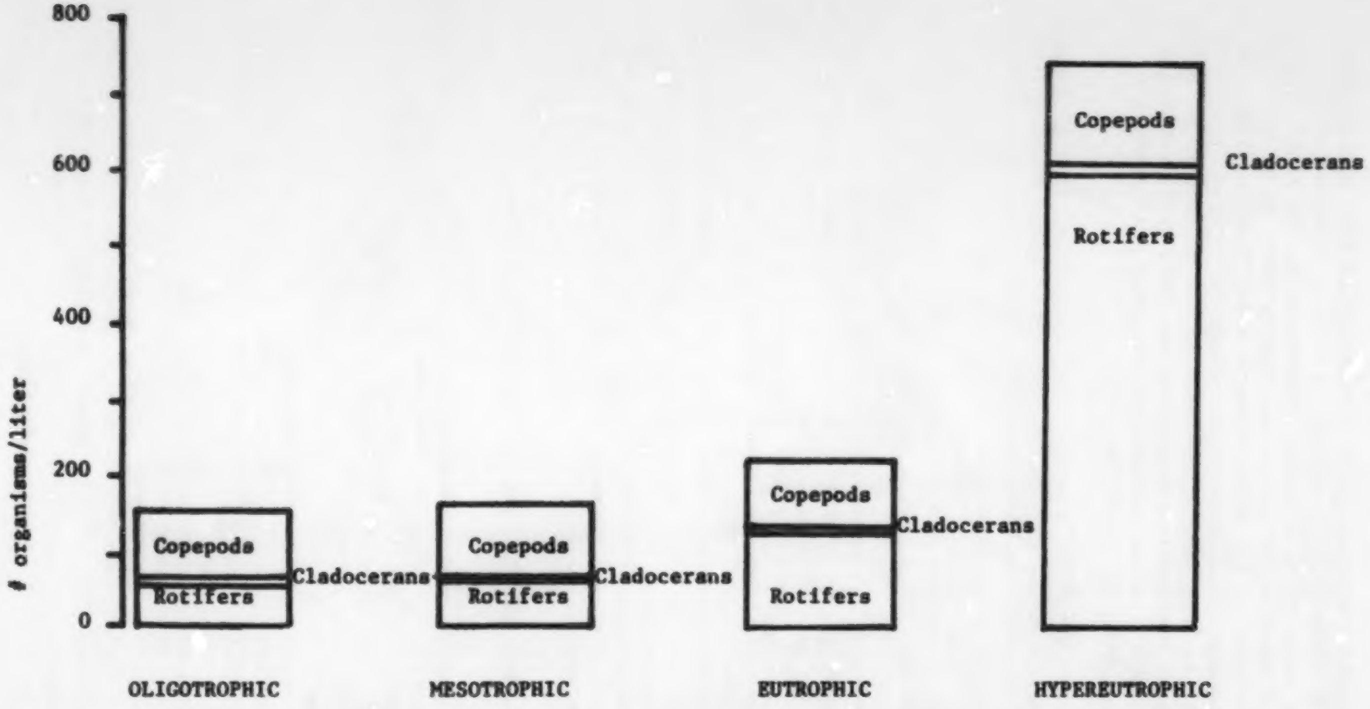

Figure 1. Midsummer partitioning of the zooplankton abundance in Florida lakes as a function of trophic state. Data from Bays (unpublished).

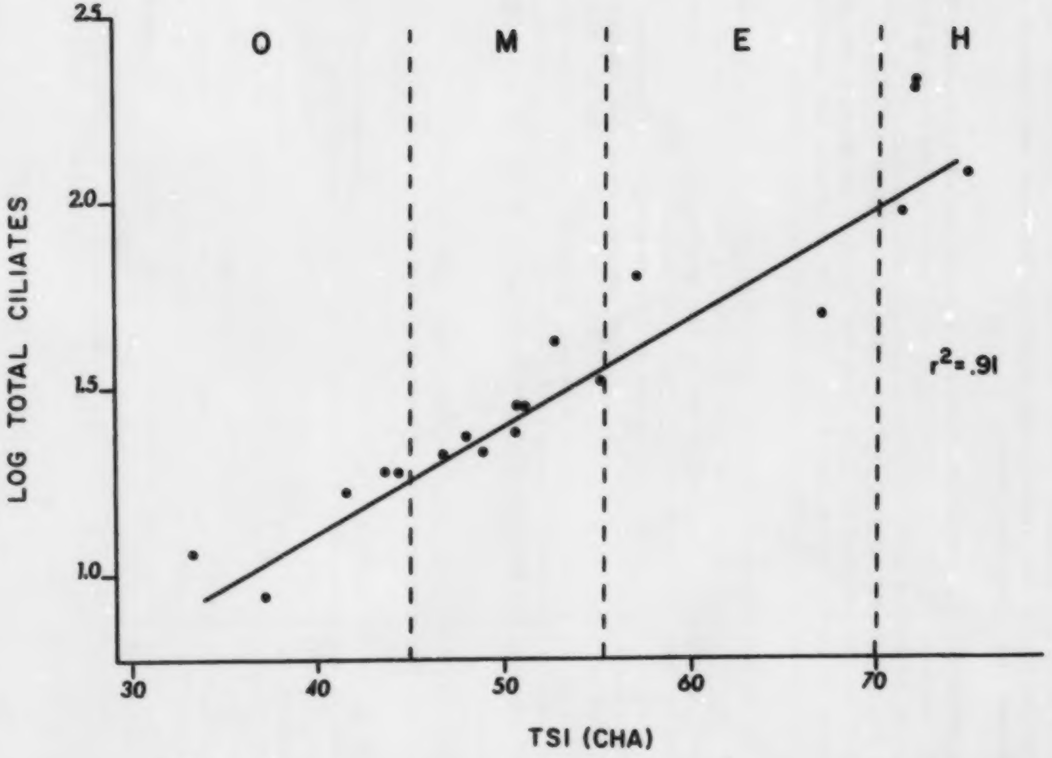

Figure 2. Relationship between the mean annual abundance of ciliated protozoans and trophic state as determined by Carlson (1977) for chlorophyll (TSI (CHA)). Figure reporduced from Beaver et al. 1980.

The abundance of macrozooplankton, presumably the most important zooplankton grazers on algae, displays a marked seasonality in Florida lakes. Unlike temperate populations which are maximal during the periods of greatest algal biomass, Florida cladocerans peak during the spring and are essentially absent during summer algal blooms. Florida cladocerans are not only smaller bodied than temperate taxa, but, unlike the latter, they are largely absent during periods of peak algal biomass. Thus, zooplankton in subtropical systems may not be as important for controlling algal composition and biomass as has been demonstrated for temperate lakes.

FISH. Eutrophication in temperate systems is accompanied by a shift in the fish fauna to favor perch (*Perca flavescens*) and other planktivorous and benthivorous species including carp (*Cyprinus carpio*) and catfish (*Ictalurus nebulosus*). The fish response in subtropical lakes is markedly different, explainable in part by the absence of carp from the Florida peninsula and the increased importance of phytophagous species. In both temperate and subtropical lakes, the importance of catfish increases during eutrophication.

Typically, the importance of largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) declines with increasing eutrophication in Florida lakes favoring a fish fauna dominated by two predominantly phytophagous species, gizzard shad (*Dorosoma cepedianum*) and threadfin shad (*Dorosoma petenense*), with catfish (*Ictalurus nebulosus*) as the principal subdominant (Figure 3). In hypereutrophic systems such as Lake Apopka, shad may constitute greater than 80% of total fish biomass (Huffstutler *et al*. 1965). Thus, while the importance of zooplankton may be reduced in subtropical lakes relative to temperate lakes, the overall impact of heterotrophic grazing on algae may be greater in subtropical systems due to the presence of phytophagous fish.

IMPLICATIONS OF TEMPERATE-SUBTROPICAL DIFFERENCES IN THE STRUCTURE OF GRAZER COMMUNITIES

The filtering rates of macrozooplankton such as *Daphnia* are not uniform but have been shown to increase with increasing body size (Ryther 1954, Richman 1958) and increasing water temperature (Burns 1969). In addition, the size of algae consumed is also directly related to zooplankton body size (Brooks and Dodson 1965). While large zooplankton such as *Daphnia* are unquestionably the principal algal grazers in temperate lakes macrozooplankton in subtropical systems do not graze algal cells as large as that consumed by temperate zooplankton due to their smaller maximum body size, but their filtering rates should be faster than that of comparably sized temperate taxa as a result of higher water temperature. We are presently conducting monthly *in situ* grazing experiments in order to assess the importance of zooplankton body size versus water temperature on the ability of zooplankton to control algal populations in Florida lakes.

While the abundance of macrozooplankton generally parallels that of algae in temperate lakes, an inverse relationship between macrozooplankton, especially cladocerans, and algae is commonly observed for Florida lakes. Florida cladocerans are maximal during the spring and absent from all but the deepest lakes during the period of greatest water temperature (29 - 31°C) and algal abundance. The general absence of cladocerans during periods of possible physiological stress but maximal algal biomass coupled with the fact that subtropical zooplankton are smaller than comparable temperate taxa suggests that

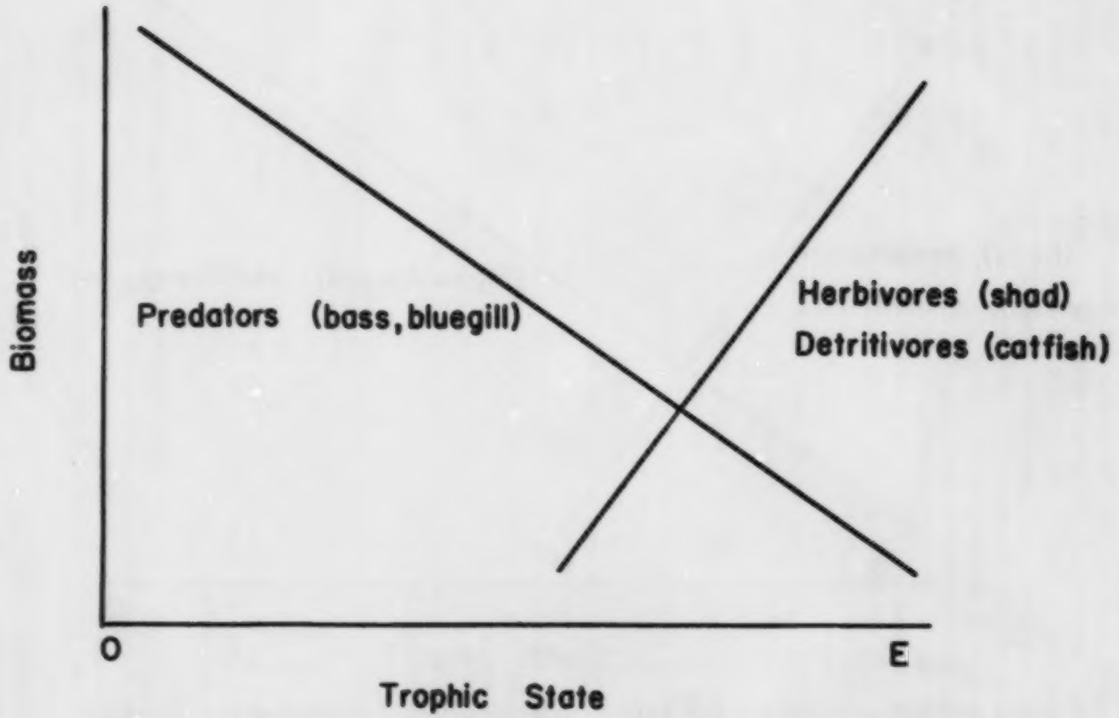

Figure 3. Generalized fish replacement series for subtropical Florida lakes as a function of lake trophic state.

the overall importance of zooplankton as algal grazers in subtropical lakes is significantly less than that documented for temperate lakes.

The greater importance of small macrozooplankton and microzooplankton in subtropical lakes, coupled with the higher turnover rates of microzooplankton (Allan 1976) and their greater nutrient excretion rates per body weight than observed for larger zooplankton (Hargrave and Geen 1968), suggest that, although the overall importance of zooplankton as grazers on net plankton may be reduced in subtropical systems, their role as nutrient cyclers should be greater than that expected for comparable temperate systems. Rather than reducing the biomass of net plankton via grazing, Florida zooplankton may enhance net plankton biomass by increasing nutrient availability and by reducing competition with nannoplankton and bacteria via grazing. This interpretation is supported by the recent in situ grazing experiments of Crisman et al. (1980) which demonstrated that, although the grazing efficiency of zooplankton on algae decreases with decreasing body size, the grazing efficiency on bacteria increases dramatically (Figure 4).

In spite of the fact that zooplankton appear to be of lesser importance as algal grazers in subtropical systems, the overall grazing impact of the heterotrophic community on phytoplankton in the subtropics may be equal to if not greater than that documented for temperate lakes due to the presence of phytophagous fish such as shad in the former systems. Macrozooplankton are the principal algal grazers in temperate systems, thus the impact of grazers on phytoplankton should decrease with increasing eutrophication associated with increased predation intensity of planktivorous fish on large zooplankton (Figure 5). While heterotrophic grazing on phytoplankton would be lower in subtropical than in temperate oligotrophic systems due to the presence of only smaller sized zooplankton as algal grazers, the presence of only minor changes in both the composition and abundance of macrozooplankton with increasing eutrophication coupled with the domination of fish faunas in eutrophic lakes by phytophagous fish such as shad suggest that heterotrophic grazing should increase with the eutrophication of subtropical systems rather than decrease as observed for temperate systems.

Finally, while heterotrophic grazing on phytoplankton appears to be dramatically different in temperate and subtropical lakes, a number of important questions remain to be answered regarding the latter systems. We know that large zooplankton are the principal algal grazers in temperate lakes and that the role of large zooplankton in the subtropics is replaced by smaller zooplankton and phytophagous fish (Figure 6). We are now turning our attention to the following questions:

1. Grazing Rates. We are particularly interested in determining the grazing rates of subtropical zooplankton and shad on net plankton, nannoplankton, and bacteria and whether heterotrophic grazing rates for subtropical systems are similar to rates calculated for comparable temperate systems.

2. Differential Digestion. The question is whether zooplankton and shad affect algal composition in the same way through differential digestion of phytoplankton species or whether one of these heterotrophs increases the food supply of the other through its inability to digest select algal taxa or size classes thereby developing a complementary feeding niche between shad and zooplankton.

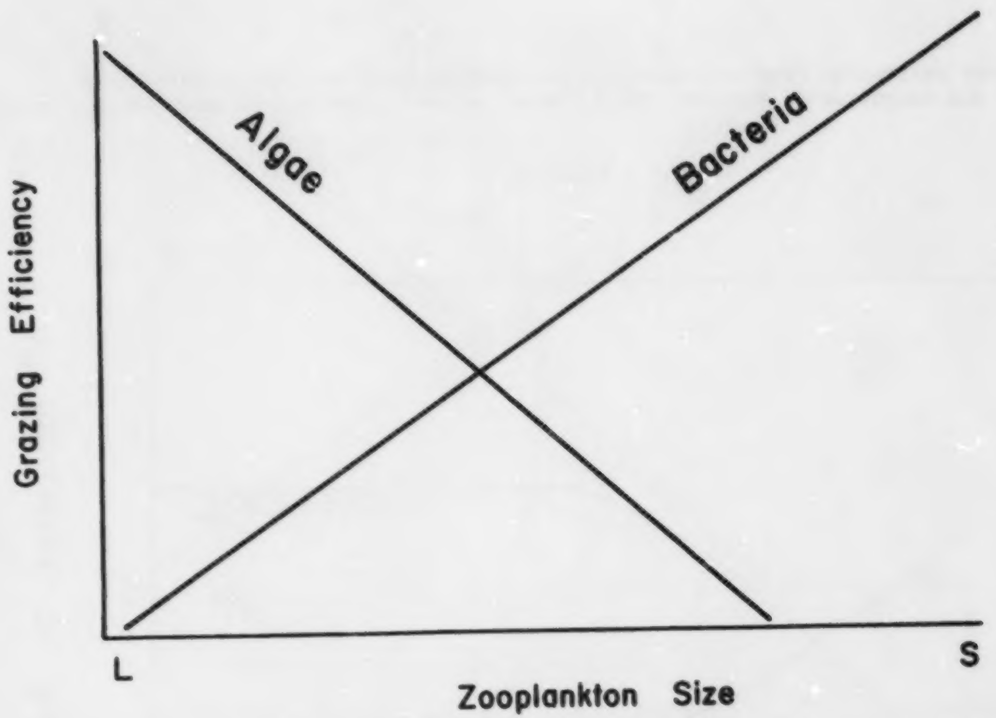

Figure 4. Variation in the importance of algae and bacteria as dietary components for various sizes of zooplankton.

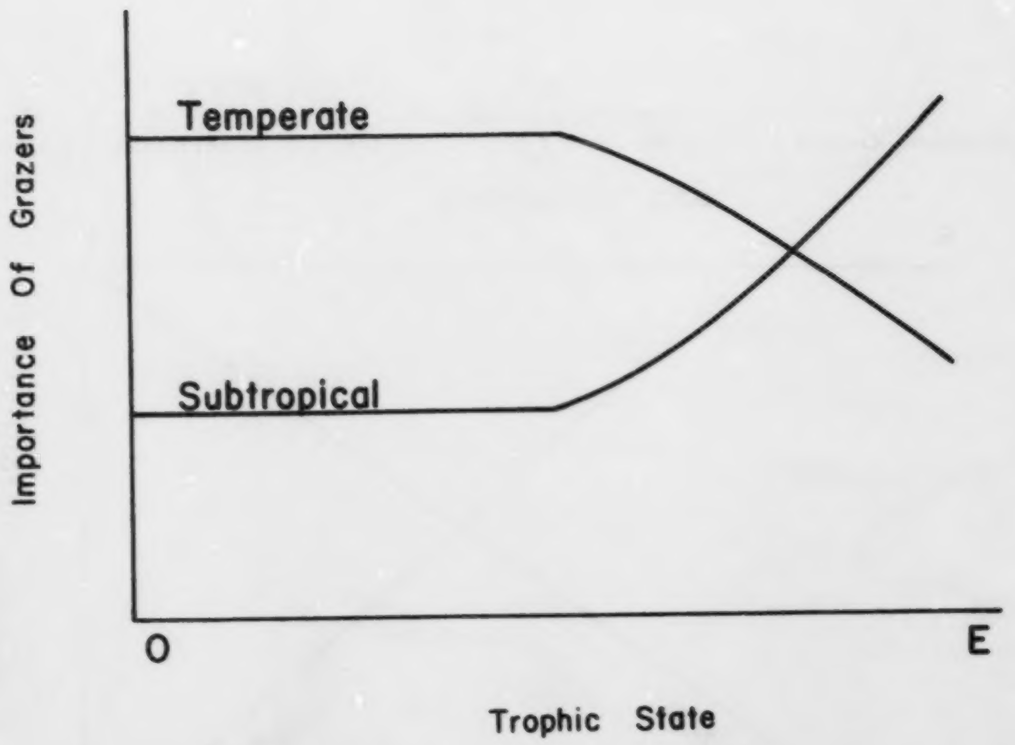

Figure 5. The generalized importance of heterotrophic grazing (zooplankton and fish) on phytoplankton along a trophic gradient for temperate and subtropical lakes.

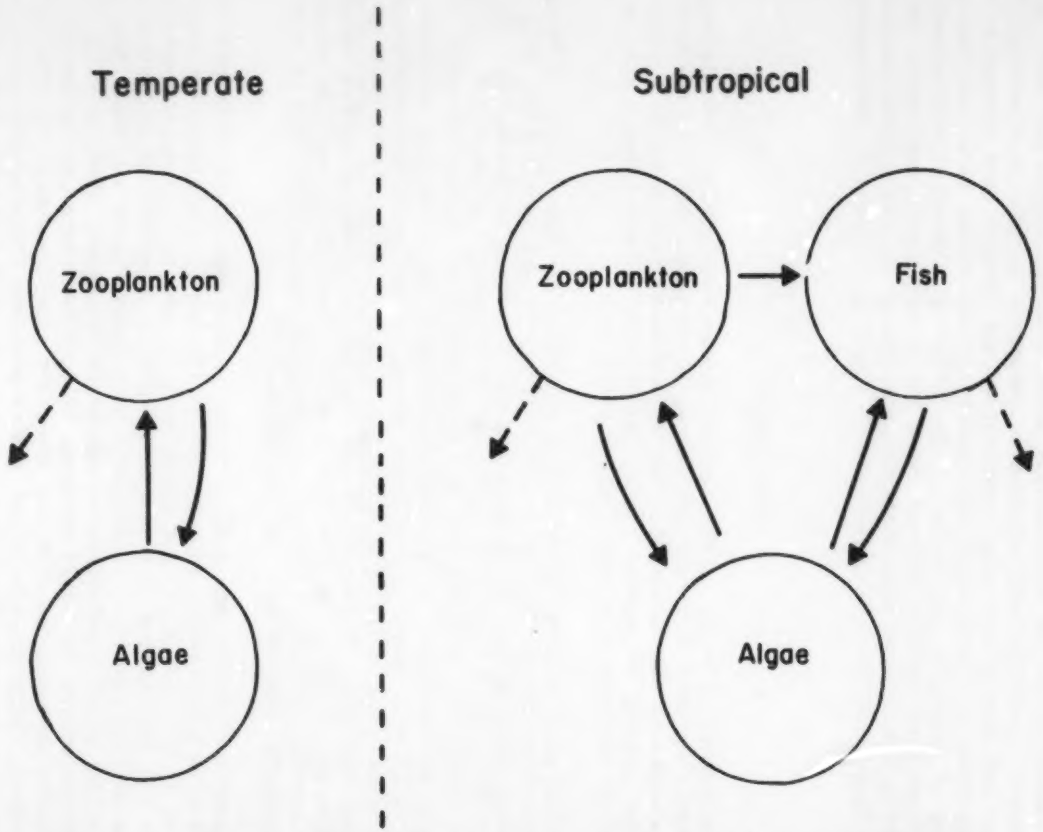
Temperate
Subtropical
Zooplankton
Algae
Zooplankton
Fish
Algae

Figure 6. Direct trophic interactions between zooplankton, phytophagous fish, and phytoplankton in temperate and subtropical systems.

3. Nutrient Cycling. We must determine if the impact of zooplankton and shad on algae in subtropical lakes is principally to reduce algal biomass through grazing or to encourage it by increasing the availability of essential nutrients such as phosphorus. In the past it was assumed that shad promoted eutrophication and that their eradication would reduce algal productivity and biomass. We must now examine this question in detail.

The complexity of the interactions between phytoplankton and their primary consumers in subtropical relative to temperate systems is dramatic. Both zooplankton and shad affect algal composition and biomass both through differential digestion of select algal cell sizes and individual taxa, and through the cycling of essential nutrients. Only following a detailed understanding of the interactions between each of these two heterotrophic components and phytoplankton and between these heterotrophs themselves can a sound management scheme be formulated for the biocontrol of algal populations in subtropical lakes.

CONCLUSIONS

The structure of algal grazer communities in subtropical lakes is much more complex than that of comparable temperate systems. Not only are zooplankton smaller in the subtropics, but phytophagous fish occur as an additional major grazing component. Thus, competition between grazers must be considered in addition to direct grazing effects.

Formulation of a broad-based policy regarding the feasibility of managing algal populations through manipulation of trophic-level interactions must consider not only regional differences in the structure of consumer populations but also differences in the principal taxa of "nuisance" algae for which the control is designed. For example, Aphanizomenon is one of the principal algal genera dominating eutrophic temperate lakes, but this alga is really not of any importance in comparable Florida lakes; rather eutrophic subtropical lakes are usually dominated by Microcystis, Lyngbya, Anabaena, or Oscillatoria. In addition, regional differences in the importance of nannoplankton versus net plankton may greatly influence the type of grazer that should be encouraged, and seasonal changes in algal dominance and the palatability of each taxa to potential grazers must be considered.

Management of algal populations through the manipulation of trophic-level interactions is a refreshing alternative to the use of algicides, but regional differences in the structure of both autotrophic and heterotrophic communities complicate the formulation of a single management plan that is applicable to most lakes in this country. Zooplankton have proven to be extremely important for controlling algal populations in temperate lakes, but their potential impact on phytoplankton is highly seasonal in both temperate and subtropical lakes. Native phytophagous fish are important algal consumers in subtropical lakes, however, their distributional limits preclude their consideration for utilization in most temperate lakes. Perhaps we should abandon the hope of a broad-based management scheme applicable to all lakes in this country, concentrating instead on regional schemes. The first step in this management process is a characterization of basic regional differences in trophic-level interactions.

REFERENCES

Allan, J. D. 1976. Life history patterns in zooplankton. Amer. Natur. 11: 165-180.

Beaver, J. R., T. L. Crisman, and J. S. Bays. 1980. Composition and abundance of planktonic ciliate communities as a function of trophic state in Florida lakes. Limnol. Oceanogr. (submitted).

Beeton, A. M. 1969. Changes in the environment and biota of the Great Lakes, p. 150-187. In G. A. Rohlich [ed], Eutrophication: causes, consequences, correctives. National Academy of Sciences, Washington.

Brooks, J. L. and S. I. Dodson. 1965. Predation, body size and composition of plankton. Science 150: 28-35.

Burnham, J. C. 1975. Bacterial control of aquatic algae, p. 120-125. In P. L. Brezonik and J. L. Fox [eds], Water quality management through biological control, Report No. ENV-07-75-1, Department of Environmental Engineering Sciences, University of Florida, Gainesville.

Burns, C. W. 1969. Relation between filtering rate, temperature, and body size in four species of *Daphnia*. Limnol. Oceanogr. 14:693-700.

Cooke, G. D., R. T. Heath, R. H. Kennedy, and M. R. McComas. 1978. Effects of diversion and alum application on two eutrophic lakes, EPA-600/3-78-033, U.S.E.P.A., Corvallis.

Cook, S. F. and J. D. Conners. 1963. The short-term side effects of the insecticidal treatment of Clear Lake, Lake County, California, in 1962. Annal. Entomol. Soc. Amer. 56: 819-824.

Crisman, T. L., J. R. Beaver, and J. S. Bays. 1980. Examination of the relative impact of microzooplankton and macrozooplankton on bacteria and algae in Florida lakes. Verh. Internat. Verein. Limnol. 21: (submitted).

Daft, M. J. and W. D. P. Stewart. 1971. Bacterial pathogens of freshwater blue-green algae. New Phytol. 70: 819-829.

Dillon, P. J. and F. H. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767-773.

Dunst, R. C., S. M. Born, P. D. Uttormark, S. A. Smith, S. A. Nichols, J. A. Peterson, D. O. Knauter, S. L. Serns, D. R. Winter, and T. L. Wirth. 1974. Survey of lake rehabilitation techniques and experiences. Tech. Bull, No. 75. Wisc. Dept. of Natur. Resources, Madison. 179 p.

Fast, A. W. 1979. Artificial aeration as a lake restoration technique, p. 121-132. In Lake restoration, EPA 440/5-79-001, U.S.E.P.A., Washington.

Haney, J. F. 1971. An *in situ* method for the measurement of zooplankton grazing rates. Limnol. Oceanogr. 16: 970-977.

Haney, J. F. 1973. An *in situ* examination of the grazing activities of natural zooplankton communities. Archiv. Hydrobiol. 72: 87-132.

Hargrave, B. T. and G. H. Geen. 1968. Phosphorus excretion by zooplankton. Limnol. Oceanogr. 13: 332-342.

Hrbacek, J. 1964. Contribution of the ecology of water-bloom-forming blue-green algae *Aphanizomenon flos-aquae* and *Microcystis aeruginosa*. Berh. Internat. Verein. Limnol. 15: 837-846.

Hrbacek, J., M. Dvorakova, M. Korinek, and L. Prochazkova. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verh. Int. Verein. Kimnol. 14: 192-195.

Huffstutler, K. K., J. E. Burgess, and B. B. Glenn. 1965. Biological, physical, and chemical study of Lake Apopka, 1962-1964. Florida State Board of Health, Jacksonville.

Kerfoot, W. C. 1974. Net accumulation rates and the history of cladoceran communities. Ecology 55: 51-61.

Lynch, M. 1979. *Aphanizomenon* blooms: alternate control and cultivation by *Daphnia pulex*. *In* W. C. Kerfoot (ed), Evolution and ecology of zooplankton communities, ASLO Special Symposium No. 3.

Porter, K. G. 1977. The plant-animal interface in freshwater ecosystems. Amer. Scient. 65: 159-170.

Porter, K. G. 1975. Viable gut passage of gelatinous green algae ingested by *Daphnia*. Verh. Inter. Verein. Limnol. 19: 2840-2850.

Porter, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature 244: 179-180.

Richman, S. 1958. The transformation of energy by *Daphnia pulex*. Ecol. Monogr. 28: 273-291.

Ryther, J. H. 1954. Inhibitory effects of phytoplankton upon feeding of *Daphnia magna* with reference to growth, reproduction, and survival. Ecology 35: 522-533.

Safferman, R. S. and M. E. Morris. 1964. Control of algae with viruses. J. Amer. Water Works Assoc. 56: 1217-1224.

Schindler, D. W. and G. W. Comita. 1972. The dependence of primary production upon physical and chemical factors in the small senescing lake, including the effects of complete winter oxygen depletion, Arch, Hydrobiol, 69; 413-451.

Shapiro, J. 1979a. The need for more biology in lake restoration, p. 161-168. In Lake restoration, EPA 440/5-79-001, U.S.E.P.A., Washington.

Shapiro, J. 1979b. The importance of trophic level interactions to the abundance and species composition of algae in lakes. Presented to Workshop on hypereutrophic ecosystems, Int. Assoc. Theor. Appl. Limnol., Sweden.

Vollenweider, R. A. 1968. Water management research. DAS/CSI/68.27. OECD, Paris. 183 p.

Webster, K. E. and R. H. Peters. 1978. Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspensions. Limnol. Oceanogr. 23: 1238-1245.

Welch, E. B. 1979. Lake restoration by dilution, p. 133-140. In Lake restoration, EPA 440/5-79-001, U.S.E.P.A., Washington.

EXTRACELLULAR METABOLITE INVOLVEMENT IN PLANKTON COMMUNITY STRUCTURE*

Kathleen Irwin Keating

Department of Environmental Science
Cook College
Rutgers, The State University of New Jersey
New Brunswick, New Jersey 08903

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INTRODUCTION

With the inclusion of "biological approaches" to algal management and control techniques, we seem finally to have acknowledged the obvious, inherent, biological nature of cultural eutrophication. While it would be irrational to abandon the chemical and engineering approaches which have served us in the past, it would be equally irrational to ignore the promise that biological intervention (biomanipulation, or biological programming) offers for the future. It is likely that practical, synthesized, approaches will employ all three.

To accomplish such goals will require a considerably higher degree of flexibility than has heretofore been evidenced. For example, as we explore the structure of the plankton community, we must critically examine the concepts we bring with us from the study of terrestrial ecology. A terrestrial ecosystem is not the same as an aquatic one. Niches may be the same—but habitats are surely different—and (most important because we choose to forget it) the structure of an ecosystem also depends upon the proportional significance, the relative influences, of various components of these two. It is here (to the continuing consternation of successful management) that the differences between terrestrial and aquatic ecosystems are overlooked.

Consider. The interplay of grazing (predation) and chemical defense (antibiosis) exists in both terrestrial and aquatic systems, but I would contend that the relative significance of these two mechanisms moves toward a balance, or even a reversal, as one leaves the terrestrial system for the aquatic. The influence of antibiosis (mediated by biologically active extracellular metabolites) increases in the aquatic system without necessarily lessening the influence of grazing.

PERSPECTIVE: ALLELOPATHY, PROBIOSIS ANTIBIOSIS (BIOCHEMICAL WARFARE)

Allelopathy, in vogue at present, has been an accepted terrestrial phenomenon for some time. The concept was first presented by Stickney and Hoy in 1881 when they described their studies of the black walnut, but it was only in 1937 that Mölish coined the term to label the many known examples of both positive and negative (probiotic and antibiotic) plant-to-plant effects.

The terms antibiosis and probiosis are more suitable in the present discussion because they can conveniently replace allelopathy while also serving in discussions of extracellular metabolite-mediated interactions of many non-plants. But—allelopathy is one part of this complex array of biological interactions, and semantics need not arbitrarily exclude that concept.

It is critical that the roles of pro- and antibiosis be reevaluated. These are commonplace phenomena, their inclusion in an organism's bag of tricks is not "the exception"—it may well be "the rule."

Poison ivy is notorious for keeping people away with an extracellular metabolite, and plants in general employ metabolites (both extracellular and unequivocally cell-bound) to discourage predation. One commercially exploitable example of such terrestrial antibiosis is the insecticide pyrethrum, a metabolic product of chrysanthemums, which has proven highly successful. There are dozens of pesticides of similar origin (review: Cruickshank and Perrin, 1964). Another rarely considered example of commercially significant antibiosis is that myriad of drugs we label "antibiotics," and—lest we leave a list of well-known examples of terrestrial extracellular metabolite effects without a convincing example of probiosis—consider that vitamins are obviously biologically active and some (especially water solubles) can be categorized as extracellular in the broader sense (infra). Actually, many of the prokaryotic products we refer to as "fixed nitrogen" are extracellular in the narrow sense, and a challenging case can be made for urea, uric acid, and all other "waste" products. The production of extracellular products of metabolic origin is, in fact, quite commonplace. Yet these products are automatically relegated to esoterica.

Obvious examples of extracellular metabolite-mediated pro- and antibiosis also abound in aquatic ecosystems. The presence of both allochthonous and autochthonous vitamins has been repeatedly noted. Proteins, carbohydrates, lipids, alcohols, and hormones have also been reported (Stewart, 1974), and phytoplankters, bacteria, macrophytes (Wetzel, 1969), and zooplankters (Krueger, 1980; Shapiro, 1980) have been implicated as in situ producers. The most notorious instances, however, of extracellular metabolite-mediated events in aquatic ecosystems are the infamous red tides common in coastal areas around the globe. These minor disasters involve all sorts of biologically active metabolic substances—from the endotoxins of Gonyaulax tamarensis and exotoxins of Gymnodinium breve to the postulated soluble products of various bacteria. That metabolic products play a critical role in the destruction wrought by red tides is underlined by the recent implication of isolation, due to layering or to other physical restriction of water movement, in the initiation of a red tide event (LoCicero, 1975). Isolation concentrates both organisms and metabolites.

It is useful at this point to introduce and clarify the dichotomy of interpretations which exists for the term extracellular metabolites—especially as it is applied to aquatic organisms. Since Krogh and Lange (1930) first questioned Putter's (1908) theories concerning the organics given off by phytoplankters, there has been an open question as to whether the list of bio-active extracellular metabolites of phytoplankters should a) include only those products actively excreted during healthy growth (sensu Fogg, 1953), or should b) also include those products leaked out of senescent and, or, moribund cells, or mainly emancipated when dying cells lysed (sensu Lucas, 1947). While there is an obvious opportunity for a meaningful distinction to be made (especially in *in vitro* experiments) between these two types of metabolite liberation (and there is always a useful place for a philosophical and, or, semantic discussion of this question), in aquatic systems the argument is (at least for the present state of the art) misleading in management terms. Once released, all soluble metabolites are in the same water with the same opportunities to affect (negatively or positively) any, and all, living creatures in that water.

In terrestrial examples of pro- or antibiosis the distinction between these mechanisms of metabolite release is, perhaps, more critical. Cell-bound material in a plant usually does not significantly affect another plant or some animal unless the first is eaten (or otherwise internalized) by one of the second. Cells may die and lyse in place but soil, unlike water, tends to restrict rather than to encourage the movement of metabolic products. The point? Terrestrial systems are not aquatic systems. Extracellular products (leaked or lysed) play a more active role in the structuring of aquatic systems. It is the nature of water to dissolve substances. It is the nature of dissolved substances to move freely in water—contacting all creatures in that water. Many biologically active metabolites are leaked into the water, many are lysis-released, but once released as soluble products, all are equally capable of making contact with some sensitive organism. As with terrestrial organisms, biologically active metabolites which remain cell-bound (even after lysis) could exercise their influence only if somehow internalized by another organism.

HISTORY

The complicated web of intra- and interspecific, intra- and intertrophic level, metabolite exchange, which Johnstone, et al. (1924) labeled "group symbiosis on a grand scale," has undoubtedly challenged scientists for centuries; but it was not until 1908 that Putter first committed an opinion in re its significance in aquatic systems to paper. He suggested that aquatic organisms, including fishes, are generally nutritionally dependent directly on the store of dissolved organic substances (mainly phytoplankton metabolites) in natural waters. Probably because his statement was somewhat uncompromising, it was met with strong opposition, and Fogg (1962) suggests that the ready refutation of Putter's thesis, especially by Krogh, et al. (1930) was a major factor in the long-term neglect of extracellular metabolites by most early twentieth century limnologists. Protozoologists, however, were enthusiastically committed to the study of its impact on their sphere of interest, and their work provided much of the basis for present day limnological interest in the subject.

Investigators such as Woodruff (1913) and Robertson (1921a; 1921b) sought and found examples of extracellular metabolites which affected the growth patterns of their infusoria cultures. Robertson proposed an autocatalytic substance, required at specific concentrations, as the explanation for the increase in reproduction noted when the cell volume/medium volume was raised. Unfortunately, since his cultures were bacterized, his "X" factor (a thermolabile organic) cannot be certainly tied either to the contaminating bacteria or to the target protozoa. Regardless of its exact origin, the biological activity of the metabolic substance was demonstrated. He did attempt to clarify the role of bacterial contamination—not by elimination of, but rather by enrichment of, bacterial growth. Johnston (1933) discounts Robertson's claims, relegating the noted effects to nutritional variations resulting from possible differences in bacterial populations. Since Robertson's parallel cultures were established with inocula from the same "young parent" cultures, and since his results consistently show a higher reproductive rate in higher cell volume/medium volume tests, the coincidence level required to establish Johnston's argument is unrealistic; i.e. Robertson's demonstration must be recognized as valid.

In 1909 Woodruff (1913) noted an autoinhibiting effect of Paramecia in "uncontaminated" cultures. He also noted that the medium of the Paramecia had a somewhat toxic effect on Hypotrichida which reached a population maximum in mixed cultures just before the Paramecia. He observed that a growth stimulator for the Paramecia was produced by the Hypotrichida; however, he did not take up the question of successional effects.

Harder (1917) after noting autoinhibition in bacteria, went on to demonstrate the same phenomenon in Cyanophyta. Opinions were varied, interest in algal extracellular metabolite effects was ultimately rekindled by the work on protozoa. Pearsall (1923) explained diatom periodicity as strictly nutritionally controlled. Krogh, et al. (1930) cultured bacteria-free Scenedesmus in artificial and lake water media and determined that less than 10% of the alga's metabolites were excreted into media (even this amount was suggested as due to lysis). Ironically, the greatest significance of his work to this discussion is that he succeeded in demonstrating in vitro excretion, yet his major interest was to demonstrate that Putter (1908) had exaggerated the importance of extracellular metabolites. He did not concern himself with a possible ecological significance for the extracellular materials which he had demonstrated were produced by Scenedesmus.

Usually the credit for developing the concept of extacellular metabolite involvement in the structuring of an in situ plankton community is given to Akehurst (1931). In 1931 he published his classic study of algal "toxins," redefining the word toxin as "an excretion product, or products, of undefined chemical constitution which may also serve as an accessory food and may inhibit or stimulate growth." Once expressed, this definition became the basis for virtually all subsequent work relative to pro- or antibiosis. After carefully scrutinizing records of phytoplankton blooms in a number of freshwater systems, Akehurst developed a theory of successional cycling based on "oil" and "starch" (storage products) groups. With no further experimental basis (other than indirect references to the works of Woodruff, Broom, 1929 and Allen, 1922, on the nutrition of bacteria and diatoms) he describes autoinhibition and heteroinhibition and proffers a lucid, uncomplicated, evolutionary basis for both. The only valid criticisms of Akehurst's intuitive explanation of his observations which followed were those suggesting he had over-simplified the situation. For this he can surely be excused since he had none of the sophisticated analytic facilities, and very little of the broad range of data, of present day investigators.

Repeatedly through the 1930's demonstrations of, and statements concerning, extracellular metabolites—with refutations of all—were published. Steeman-Nielson (1934) suggested that differences between marine littoral and oceanic dinoflagellates could be attributed to organic metabolites. Aleyev (1934) noted excretion of extracellular substances by algae and emphasized the role of autolysis in producing these metabolites. The protozoologists Mast and Pace (1938) reported a heat-labile, bioactive, substance produced in a bacteria-free Chilomonas culture and emphasized the effects of age, condition, and quantity of parental inoculum on the potency and direction of this autoinhibitor/autostimulator. Allee (1934) studied the effects of crowding on normal organisms and emphasized the possible role of physical contact in the inhibition of metabolism and reproduction (a forecast of some of Lefèvre et al.'s (1952) findings and of the contact inhibition studies done in cancer research today). Gause, et al. (1934) noted a genetic strain effect in the varying sensitivity of his Paramecium aurelia cultures to extracellular products. Phelps (1935) found that the lag phase of culture growth could be eliminated by use of log phase inocula (he also demonstrated that final population density was independent of inoculum size and dependent on nutrient levels, 1936).

The level of controversy concerning the significance of extracellular products in vitro or in situ, and the conflicting experimental evidences on which this controversy was based, led Phelps to warn that weak controls and dissimilar conditions (including variant strains of organisms) made futile the many attempts to prove, or to disprove, the variety of theories concerning extracellular metabolites. It is of significance that these same dangers can be pointed out in more recent publications (especially those relating to phytoplankton/zooplankton interactions) when the statements of one investigator are countered by another (see especially, but not solely, Talling, 1957; and Ryther, 1954; and Rigler, 1961; McMahon and Rigler, 1963; 1965). Parker and Bold (1961) call special attention to the danger inherent in general conclusions based on antagonism experiments wherein the two organisms involved have been isolated from different places, a caution of particular importance in lake studies (Keating, 1978a).

In 1940 the first two of Pratt's series of comprehensive studies on the extracellular metabolites of *Chlorella vulgaris* were published. He demonstrated most of the various idiosyncracies of auto- and hetero- probiosis and antibiosis which had been previously hinted at in fragmentary algal, and more comprehensive, protozoological work (*supra*).

After employing various techniques to rule out nutrition and pH as causative factors, he set out to isolate and study the specific substances demonstrating such potency in his cultures. Chlorellin, his designation for this substance, was characterized by him in 1942 as a heat-labile; water, petroleum ether, ether and ethyl alcohol-soluble substance; probably a form of organic base (Chlorellin is more potent at higher pH's) with molecules of less than 15Å which are able to pass through cell membranes. In 1943 Pratt published the last in his series of *Chlorella* articles, ascribing the antibiosis he had observed to an inhibition of the dark reactions of photosynthesis.

Pratt's intensive work with *Chlorella* and the work of a number of other phycologists (Levring, 1945, *Skelatonema costatum*; Flint and Moreland, 1946, Cyanophyceae; Denffer, 1948, *Nitzchia*; Myers and Johnson, 1949, *Chlorella*; Lefèvre, *et al*. 1948 and thereafter, a variety of algae) throughout the 1940's apparently quelled the arguments as to the existence of algal extracellular metabolites sufficiently to allow a new facet of the problem to gain eminence. The next major questions raised were (and still are) 1) whether metabolites evidenced *in vitro*, ever exist in sufficient quantities *in situ* to exert appreciable effects on natural populations, and 2) whether any ecologically significant *in situ* phenomenon can be clearly tied to soluble extracellular metabolites. Publications in the 1970's (Williams, 1971; Keating, 1977; 1978a; 1978b) have reasonably answered these questions for allelopathy. Additional research which would clearly establish the roles, and the ecological significance, of more generalized extracellular metabolite effects between and among not only the phytoplankters but also the many other modules of the plankton community is still needed.

Fogg's many studies of phytoplankton physiology have emphasized the high levels of protein in rapidly growing and reproducing cells and the high levels of stored fat, or carbohydrate (resulting, respectively, from nitrogen or phosphorus limitations) in senescent cells. This is not the sole pattern--Lewin (1956) worked with *Chlamydomonas* species which produced polysaccharides throughout the period of normal growth. Nevertheless, the common occurrence of a change in endometabolites with age is one of the bases for Fogg's concern in re the distinction between leaked and lysis-released metabolites. His point of view must be taken into account during *in vitro* work. He offers (1953) young cultures of *Anabaena cylindrica* in which as much as 50% of assimilated nitrogen is (leaked) excreted as extracellular metabolite, and in which relatively few cells lyse, as a clearcut example of his concept of extracellular metabolite production. Lefèvre and his coworkers (1964) have found not simply different, but actually opposite effects due, they believe, to secretion of different substances which alternately dominate extracellular metabolite activity. Unpublished studies from our lab substantiate these premises.

Jørgensen and Steeman-Nielsen (1959; 1961) by analyzing Chlorellin into three distinct active substances (two anti- and one pro- metabolite, as tested on *Staphylococcus aureus*—an array like that reported by Keating (1978a) have further demonstrated the wisdom of considering the mode of metabolite release as one of the many parameters which require precise monitoring in this type of research. Pratt (1943) thought he had a *single*, excreted, product--now there must be questions as to the accuracy of both of these characterizations. While essential to *in vitro* work, efforts toward distinguishing leaked and lysis-released metabolites will not provide additional management alternatives at present. With additional understanding (further research) this may change.

Interest in the *in situ* occurrence of extracellular metabolite-mediated antibiotic, or probiotic effects was evidenced in Akehurst's (1931) writings, but the intuitive nature of his theories instigated experimental efforts simply to demonstrate allelopathy *in vitro*. Proof that these metabolites might occur *in situ*, and might occur in sufficient quantity to affect other organisms, was left to investigators in the late 1940's, and thereafter.

It required the challenge of G. E. Hutchinson (1944) to stir interest in *in situ* work. After careful study and comparison of phytoplankton chemical cycles in Linsley Pond, he strongly refuted the thesis of Pearsall (1932) which contended that the periodicity of phytoplankton is determined chemically. He also eliminated temperature and light as possible singular architects of phytoplankton cycles. Then, calling attention to obscure relationships between various population patterns in different species, he implicated the interplay among complex chemical, physical, physiological, and interpopulational effects as the basis for phytoplankton succession. He warned that "the possible role of organic metabolites as inhibitors of certain species must be borne in mind." His discussion ends with a prodding statement, ". . .a population and its relation to populations of other species are likely to explain many of the apparent inconsistencies observed. . ." (see also Hutchinson, 1961).

THE PREDATOR AS VICTIM

Extracellular metabolite effects between and among phytoplankters, protozoa and bacteria, and those which also include zooplankters have been studied and reported by different groups of scientists as if they were quite unrelated phenomena—which they are not. Hardy (1935 with Gunther; 1936a; 1936b) considered the plankton as a single community, one in which phytoplankters and zooplankters (among others) interact. His theory of animal exclusion provided a dichotomous explanation for the commonly observed inverse distributional relationship between zooplankton and phytoplankton (he cites fifty years of prior examples). He hypothesized that 1) animal grazing accounted for the greatest influence on phytoplankton distribution "where phytoplankton is not very dense" (*i.e.*, mesotrophic waters), and that 2) "some excluding influence of the plants", presumably chemical in nature, accounted for the limited zooplankton populations in "dense areas of plant production" (*i.e.*, eutrophic waters). While his speculations were based on observations of marine plankton communities, they appear to be equally well-suited to the interpretation of events in freshwater communities.

Unlike the predator/prey portion of his theory, Hardy's second hypothesis, that of an "excluding influence of the plants" which limited zooplankton populations, has been neglected in the intervening years. This is partially because considerable success has been achieved in documenting the impact of zooplankton grazing on phytoplankton populations, but it is also partially because we tend to think in the terms previously established for terrestrial ecosystems (predator/prey) and to allow ourselves the privilege of benign neglect for non-conforming, additional, terms and concepts.

Perhaps the most influential statements concerning phytoplankton/zooplankton interactions (if frequency of citation is a proper gauge) following

Hardy's were those of Harvey (1945; *et al.*, 1935). He and his coworkers emphasized the importance of zooplankton grazing on phytoplankton population patterns and considered other phytoplankton/zooplankton interactions to be of minor significance to the structuring of the plankton community. Many investigators have reinforced this emphasis on zooplankton grazing— not only with *in situ* observations of the onset, duration and interdependent patterning of phytoplankton and zooplankton blooms, but also with *in vitro* studies of zooplankton feeding. While some (Anderson, *et al.*, 1955; Sládeček, 1958; Wright, 1958; Wimpenny, 1973; Berman and Richman, 1974) have indicated their belief that grazing is a sufficient explanation for the patterns they have observed; others (Riley, 1940; Pennak, 1946; Lefevre, 1950; Lefevre, *et al.*, 1952; Ryther, 1954; Mullin, 1963; McMahon and Rigler, 1965; Burns and Rigler, 1967; Burns, 1968; Stangenberg, 1968; Arnold, 1971; Stross, 1975; Porter, 1980) have indicated that additional influences must be postulated to account for some of their observations.

In evolutionary terms phytoplankters must profit from pro- or antibiosis enough to provide a selective advantage sufficient to overcome the randomized elimination of genetic drift and to justify the energy invested in lost metabolites. While the producing organism need not profit further, additional profit would enhance the selective value of losing metabolites and would increase the likelihood of this characteristic becoming widespread. For example, the competitive advantage which annually permits certain blue-greens to dominate the plankton community of a eutrophied lake (Keating, 1977) would be sufficient to justify maintenance of extracellular metabolite production, but their extracellular products also contribute to their capacity for long-term dominance (Keating, 1978a; 1978b) of a lake system, to their ability to obtain scarce trace metals, and to their capacity to withstand otherwise toxic levels of heavy metals (Provasoli, 1963; Whitton, 1965). Additionally, there is considerable basis for speculating that extracellular products contribute to the capacity of blue-greens to limit predation by rejection (Lefèvre, 1950), by inhibition of feeding (McMahon and Rigler, 1965; Mullin, 1963) or reproductive activities (Arnold, 1971), or by killing off their predators via internal cellular disruption (Ryther, 1954; Murphy, Sohi, and Fast, 1976). This spectrum of advantages, associated with one widespread trait (metabolite loss), may be the key to the incredibly long-term survival of the prokaryotic blue-greens (the origin of CO_2-fixing prokaryotes has been placed back 3.5 billion years, Schopf, 1980).

A number of empirical examples of plant/animal interactions both _in vitro_ and _in situ_ have been reported and, if comments and observations resulting from studies of the nutritional value of various algae for zooplankters are also included, there is sufficient empirical data to warrant serious consideration of the significance of algal antibiotic influences on zooplankton *in situ* (Arnold, 1971; Burns and Rigler, 1967; Edmondson, 1965, 1957; Fitzgerald, 1964; Heinle, 1969; Hutchinson, 1967; Lefèvre, 1950; Ryther, 1954; Schindler, 1971; Sorokin, 1968; Stangenberg, 1968). There is, in fact, sufficient data to suggest that the rapid *in situ* disappearance of *Cladocera* with the onset of certain blooms, especially of blue-greens, is *not* simply the result of an inadequate array of nutritionally essential macromolecules produced and stored in food organisms (Gibor, 1956; Ryther, 1954; review: Stewart, 1974). After all Arnold's (1971) *Daphnia pulex* survived, on the average, more than three weeks in cultures with no food and Cladoceran populations in lakes which produce rapidly growing blooms are likely to disappear in a matter of days (Stross, 1975; Keating, 1976). Also, there are other, edible, algal and protozoan species available even during the almost unialgal blooms of some blue-greens. These non-dominant organisms are represented by relatively low numbers, but when added to the bacteria, they are sufficient to allow the grazing necessary to satisfy the postulated nutritional inadequacies of the blue-greens. In addition, dissolved organic micronutrients exist *in vitro* (Taub and Dollar, 1964, found that the nutritional inadequacies of *Chlorella* and *Chlamydomonas* for *Daphnia pulex* were in part overcome by the addition of "bio-conditioned" water from a fish tank) and may reasonably be postulated to exist *in situ*. Since some undefined vitamins or other trace-organic growth factors are usually presumed to be the missing nutrients (there are sufficient macronutrients), the quantities required for supplementing the supposedly inadequate menu provided by a blue-green bloom dominant should be quite small.

Much of the dissolved, metabolically produced, extracellular material in natural waters, however, must be considered non-nutritional—some is probably neutral to zooplankters, some is surely detrimental. Ryther's studies (1954) of Daphnia magna feeding, for instance, suggested that there are both inhibitory metabolites which diffuse from cells of Chlorella vulgaris into media, or ambient waters, and inhibitory metabolites which are bound inside cells to be released only during gut passage and digestion. While these latter, cell-bound, inhibitors might be avoided by zooplankters, it is likely that such metabolic products as might be dissolved in ambient waters could not be similarly avoided.

Rigler and McMahon (Rigler, 1961; McMahon and Rigler, 1963; 1965) have questioned the evidence Ryther offered for the presence of these negative effectors because his proofs relied on his demonstration of an inverse relationship between filtering rates and concentrations of the food organisms, Chlorella vulgaris, Navicula pelliculosa, and Scenedesmus quadricauda. Using a wider range of food cell concentrations, they demonstrated that for their Cladocera, filter-feeding rates were directly proportional to concentrations of food cells but only below an "incipient limiting concentration" of food cells (0.3×10^6 cells/ml for their C. vulgaris), and that above the critical limiting concentration, filtering rates were essentially independent of ambient food levels.

While prior reports of a relationship between food cell concentrations and filtering rates suggested that they vary in direct proportion, Ryther's observations of an indirectly proportional variation associated with specific food organisms were not unique. Mullin (1963) reported that above a threshold concentration the filtering rates of his several species of Calanus varied indirectly with the concentration of food cells. Like

Ryther, Mullin concluded that the slower feeding rate was in part a reflection of some antibiotic effect of an algal metabolic product on the zooplankter.

McMahon and Rigler, essentially because their experimental data did not clearly confirm Ryther's work, concluded that his studies using log phase _C_. _vulgaris_ did not warrant his conclusions regarding antibiosis. _But_ they (1965) clearly did accept the existence of negative effectors, and they offered their own experimental evidence to verify certain of Ryther's interpretations of the inhibitory effects of senescent _C_. _vulgaris_ on _D_. _magna_.* They proposed both external and internal chemosensory involvements in the observed slowing of filtering rates of _D_. _magna_ in the presence of senescent _C_. _vulgaris_ cells. Without relying on isolation of antibiotic compounds, or speculation about the nature of the inhibition itself, they demonstrated the intragut location of at least some of the chemosensory capacity of _D_. _magna_.**

These events do not require involvement of "extracellular" metabolites—membrane-bound metabolites would be equally effective. It is possible that minimal external contact with (Friedman and Strickler, 1975; Richman, _et al_., 1980) or coincidental ingestion of even a few cells of an organism which carried its toxic metabolites tightly bound to membranes might not only be perceived by the Cladoceran's chemosensory apparatus, it might also (whether recognized by chemosensors, or not) produce damage which would then evidence itself as an interference with filtering or with some other essential activity. The effects on Lepidoptera of the mid gut digestion of cells of Bacillus thuringiensis (Murphy, Sohi, and Fast, 1976)—during the digestive process "harmless" proteinaceous crystals evolve into delta endotoxin (EDD) disrupting and disintegrating the epithelial cells lining the gut—offer an insect-based example of the type of damage postulated. An undesirable phytoplankter, if digested, could reasonably emulate this bacterial action, concentrating damage in the gut during passage. Stangenberg (1968), for example, has demonstrated a membrane-bound blue-violet pigment which is highly toxic to Daphnia longispina and which is released by freezing cells of Mycrocystis aeruginosa. This substance might be an example of a digestion-released toxin. The intact algal cell is apparently quite harmless to the D. longispina; i.e., this cannot be considered an example of an "extracellular" metabolite effect, and to parallel the action of the plant toxin for its insect victim, the M. aeruginosa would have to be broken up during gut passage. This adds to the difficulty of interpreting the ecological significance of this toxicity because this algae might be among those which pass intact through the gut of a zooplankter, infra.

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*Mullin (1963) reported similar negative effects related to the use of older food cultures.

**They worked out an ingeniously simple experiment in which prefeeding caused a later inhibition of filtering rates which they could associate back to gut contents.

An extraordinary need for research exists in this area. Distinguishing between extracellular (leaked and lysis-released) and membrane-bound metabolic products can be most productive in terms of determining the level, mode, and extent of the antibiotic effects, but as with the distinction between leaked and lysis-released extracellular metabolites, the careful examination of the phenomena of intertrophic level biochemical warfare ought not be too rigidly confined by semantics.

Several investigators have reported intact gut passage of algae, especially those encased in thick gelatinous sheaths (Naumann, 1918; 1921; 1923; Fitzgerald, 1964). In addition, Porter (1976) has shown that gut passage may be stimulatory (nutrients are absorbed during gut passage) to certain of the Chlorophytes. The blue-greens, therefore, which are generously endowed with gelatinous sheaths, might commonly be mechanically protected from digestion and might actually benefit (as do the Chlorophytes, supra) by being ingested. This could work to the temporary advantage of that zooplankter which inadvertently ingested an organism carrying toxic, or inhibitory, metabolites tightly bound to membranes by sparing the animal exposure to the toxin. But it would not protect the zooplankter from extracellular metabolites if such were leaked through cell membranes and sheaths during gut passage, and intact passage of phytoplankters could prove to be ultimately disadvantageous to the zooplankter if selective gut passage were to enhance the growth of the antagonistic organisms (per Porter's findings).

Many filamentous forms of phytoplankter, especially of blue-greens, are dimensionally ill-suited to ingestion by the filter feeding apparatus of the Cladocera, and Lefèvre (1950) and Burns (1968) have observed the active ejection of blue-greens by Daphnia. Burns suggested that this ejection may be due to a chemical incompatibility. Certainly, the ejection mechanism suggests eigher physical or chemical recognition (or both) of the expelled organism as one which is undesirable.

Actually, the ingestion of phytoplankters with heavy gelatinous sheaths, even if it does not produce contact with a biologically produced toxin, may still prove detrimental to zooplankters. Since instances of excessive concentrations of heavy metals in freshwater systems are being constantly recorded, and since Fogg and Westlake (1955) and Murphy, _et al_. (1976) have demonstrated a capacity of the sheath materials (extracellular polypeptides) of blue-greens to chelate, or to adsorb, heavy metals, increased exposures to heavy metals is inevitable for those zooplankters which ingest blue-greens.

There are reports (Arnold, 1971; Schindler, J.E., 1971; Schindler, D.W., 1968; Sorokin, 1968) that some blue-greens are ingested (usually at a lower rate than the more desirable food species) and that some are at least partially assimilated by some Cladocerans with no apparent immediate adverse effects. It is important, however, to keep in mind that most experiments were of brief duration (some using ^{14}C tracers) and were done with bacteria present, under relatively undefined, uncontrolled, culture conditions--reflecting the state of the art of the times. Again, extensive study is needed.

Arnold's (1971) longest-term experiments provided the strongest indications of the adverse effects of selected phytoplankters on zooplankters to date. His life tables displayed gross interferences with longevity and fecundity. In fact very low food concentrations (when undesirable species were the "food") produced longer life spans and higher reproductive rates than did higher* concentrations. Actually, the longevity of the _Daphnia pulex_ he employed was greater in sterile water cultures with no food than it was in many of his _Daphnia pulex_ cultures with food. Of course the D. pulex in neither of these conditions approached the longevity or fecundity displayed by his controls—fed Ankistrodesmus falcatus or yeast.

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*Higher concentrations could not be interpreted as excessive since they were in the same range as the most productive concentrations of _Ankistrodesmus falcatus_ and yeast which were used as foods in control cultures.

ANTIBACTERIAL EFFECTS OF EXTRACELLULAR METABOLITES

Aubert and his colleagues (1963-1975) have provided extensive and coordinated *in situ* studies of the extracellular metabolite-mediated effects between and among the various planktonic organisms. For example, their studies have developed a strong *in vitro* case for the algal antibacterial effect they believe is demonstrated *in situ* by rapid dissipation of sewage bacteria in the Mediterranean Sea. Though they have clearly included the algae among those organisms secreting antibacterial substances, they have not excluded the possibility that their role in coliform elimination may be minor in comparison to the role of marine bacteria (as Moebus, 1972a, 1972b, 1972c, has suggested) or to the more commonly proffered explanations of anti-coliform activity which consider sedimentation, dispersion, predation, and lack of reproduction to be the critical factors. Sieberth (1964) with less *in vitro* evidence has correlated the anti-coliform activity of sea water samples from Narragansett Bay directly with the irregular blooms of *Skeletonema costatum* and has presented a less strenuous *in vitro* argument to substantiate his thesis; *i.e.*, his cultures require bacteria and additional phytoplankters to develop a strong antibiotic effect (his axenic cultures of *S. costatum* show no anti-coliform activity).

The work of several others has also served to substantiate the *in situ* antibacterial activity of algae. Steeman-Nielsen (1955), using light and dark bottle techniques to measure oxygen consumption, noted that the algae growing in "light" bottles inhibited bacterial respiration and thus interfered with measurement techniques. Jørgensen (1962) isolated chlorophyllides from filtrates of a variety of naturally growing algae and found them to be inhibitors of bacterial growth. Jones (1959) found the soluble organic extracts of sea water collected during a "red tide" bloom of Gonyaulax polyhdera to be highly antibacterial. Interestingly, he noticed a zone of stimulation surrounding the zone of inhibition on agar plates which is reminiscent of certain effects of plant hormones (Bentley-Mowat and Reid, 1969), indicating stimulation at low concentrations, and inhibition at high concentrations. This is only one example of the complicated array of activity to be expected from any single extracellular metabolite, and a single organism may be expected to produce a variety of extracellular products! Jones' observation might also have been of the dilution-stimulation Pratt (1942) thought he was witnessing in his Chlorella experiments, or it might have been of several extracellular metabolites as Jørgensen and Steeman-Nielsen (1961) and Jørgensen (1962) proved Pratt's (1940, 1942, 1943) "Chlorellin" to be--or it might have been an indication of some totally unknown phenomenon peculiar to this alga.

In 1966 Duff, Bruce and Antia surveyed the antibacterial range and potency of Bacillariophyceae, Chrysophyceae, and Cryptophyceae and concluded that these are more generally potent antibacterially than are the Chlorophyceae or the prokaryotic blue-greens. Their algal samples, used after drying as a source of active substance, were harvested from axenic mass cultures derived from a variety of geographic origins. The assay bacteria were from type collections, or were fresh isolates from the sea. Two ecologically significant theses were proffered: 1) the selective activity of their algal strains against Gram-positive bacteria (especially Staphylococcus) may account for the prevalence of Gram-negative bacteria in the seas (also suggested by the work of Saz, et al., 1963), and 2) the specific value of the antibacterials, in terms of natural selection, may be to control epiphytic bacteria. This epiphytic association would eliminate the dilution arguments against in situ antibiotic effects.

Other work with epiphytic associations includes that of Fitzgerald (1969) who found that Cladophora in nitrogen-poor situations were free of epiphytes (including bacteria and other algae). An evolutionarily selective value may be found in the coincident excretion of substances toxic to epiphytes at that time when the Cladophora is experiencing nutritional stress. Similarly, McLachlan and Craigie (1964) found that Fucus vesiculosis produced an inhibition of unicellular algae (likely epiphytes and competitors), and Jørgensen (1956) demonstrated an inhibition by planktonic diatoms and Chlorophyta on epiphytes.

In 1970 Davis and Gloyna determined that axenic cultures of freshwater green and blue-green algae were mildly inhibitory to enteric bacteria in general and decidedly inhibitory to pathogenic forms. Their parallel experiments in waste stabilization ponds produced similar results; however, the endemic bacterial communities of these ponds provided cultures of Flaveobacterium and Brevibacterium which, they noted, were more effective than the algae tested in eliminating enteric forms—reminiscent of the findings of Aubert (1963-1975) and Moebus (1972a; 1972b; 1972c). Finally, although Fogg expressed the opinion in 1962 that "when vigorously growing cultures of algae are exposed to contamination, it is often observed that relatively few bacteria develop, an effect which could conceivably be due to their suppression by antibacterial agents," he was still dissatisfied in 1977 with the experimental proof of the significance of in situ algal extracellular metabolite-mediated pro- or antibiosis.

CONCENTRATION AND DILUTION OF EXTRACELLULAR METABOLITES

Schwimmer and Schwimmer, in 1964, offered an intriguing discussion of the various documentations of algal toxicosis in vertebrates, including humans. More recently Quick (1973) found the "whirling death" fish kills in Biscayne Bay to be due to the presence of an *Anacytis sp*. In 1974 Aziz obtained a diarrhea toxic from a new strain of *Microcystis aeruginosa*. Considering these relatively direct examples, and considering the well-known, well-documented, effects of toxic "red tides" (Gilbert, 1974) and of the "fast death" factors produced by certain strains of *M. aeruginosa* and *Anabaena flos-aquae* (Gorham, 1964; Fogg, 1962), it would appear reasonable to assume that extracellular metabolites do occur in sufficient quantities *in situ* to cause metabolic reactions in other organisms. But unequivocal proofs relative to *in situ* potency are few, and as such they have not convinced most commenting scientists that extracellular products play an active role in the general structuring of ecosystems.

Much additional coordinated study of *in vitro* and *in situ* extracellular metabolite-mediated biological activity is needed. Fogg (1966) cautions (a) that stationary numbers in nature and in culture may not be the overt manifestation of similar phenomena; and (b) that the massive release of some metabolites "occurs only under particular circumstances which do not necessarily occur in laboratory cultures, but which may occur regularly under natural conditions." This warning follows his commentary on experiments with glycolic acid excretion, wherein natural marine and freshwaters showed the results of very high excretions of fixed carbon while cultures showed insignificant levels (*infra*). The significance of the quantity of extracellular release, however, should not be overemphasized (Aaronson, 1978; Sharp, 1977). A lack of evidence for the excretion of large quantities of metabolite does not suggest a lack of activity (Sharp, 1978). One need only consider the microquantities of plant hormones necessary to promote growth, flowering, abscission, *etc.*, to appreciate this.

The commonly observed exaggerated concentrations of metabolic products in or from cultures, on the other hand, can easily become a critical flaw in the designation of *in vitro* instances of pro- or antibiosis as "ecologically significant." Berland, *et al.*, (1972) warned of this after they found that in order to demonstrate an antibacterial effect on their most sensitive assay organism by filtrates of *Stichochrysis immobilis*, they had to use a twenty-fold concentration of the filtrate, and Kroes (1971, 1972) found that in similar circumstances a ten to twenty-five-fold concentration was necessary. Kroes concluded that the four types of extracellular inhibitors he found were not ecologically significant because of this concentration requirement, and he suggested pH effects as the really significant factor in observed instances of antibiosis. To properly consider the doubts raised by concentration requirements, one must consider Fogg's warnings (1966, *supra*) and the more recent report of Ignatiades and Fogg (1973) that, depending on culture conditions, anywhere from 2.1% to 87.4% of the total carbon fixed by a single organism may be excreted. Exaggerated concentrations of metabolites, then, may occur *in vitro* or *in situ* (or in both)—guaranteeing a discomforting array of plausible explanations for experimental results.

A few values, if noted with proper perspective, can be enlightening. Attempts were made as early as 1930 to determine precisely what portion of fixed carbon (or nitrogen) is excreted by various algae. Braarud and and Føyn (1930) estimated that a marine *Chlamydomonas* released approximately 30% of its organic production. This figure compares reasonably with Lewin's 1956 estimate that *Chlamydomonas* excreted from 40-60% of its total organic product into its mucilaginous capsule, and with the 35-40% excretion estimate of Antia, *et al*. (1963). In contrast Fogg reported (1966) a 95% excretion level in fresh waters under certain circumstances, but found that the more usual levels ranged between 7% and 50% (usually varying inversely with population density). He suggested that similar levels could be expected in marine waters. But in 1977 he expressed dissatisfaction with the many published attempts to quantify *in situ* production.

Hellebust's (1965) *in situ* and *in vitro* estimates were somewhat lower for "healthy" organisms than were those of Fogg or Antia. Hellebust distinguished healthy (4-16%) and senescent (17-38%) colonies. In contrast Nalswajko (1966) reported *in vitro* excretion for healthy organisms at less than 2%. However, Nalewajko used young log cultures and allotted one hour for labelling (early products); while Hellebust used young log cultures and allotted four days for labelling (full array of products with probable recycling). Thus, a superficial comparison which suggests great disparity in data can be quite misleading. As Fogg (1962) commented, "Measurements of the amounts of extracellular material can have no precise significance unless the physiological history of the system and its environmental conditions are defined." Again--a need for additional research is demonstrated.

VITAMINS AS EXTRACELLULAR METABOLITES

Provasoli (1963) suggested three possible areas of in situ metabolite activity: 1) the removal, or deactivation, of inhibitions; 2) the production of specific inhibition; and 3) the production of necessary nutrients, or growth factors. Much study has been devoted to a portion of his third category. Vitamins and other "growth factors" are required not only by animals, but also by more than 50% of the algae (Provasoli, 1963; personal communication, 1975; Saunders, 1957). They are also well established as products of algal metabolism (Robbins, et al., 1951; Carlucci and Bowes, 1970a; 1970b; 1972; Bentley, 1958). The effects of vitamin availability, and utilization, therefore, are a specialized form of probiosis.

Excretion, lysis, and decomposition each play a part in releasing those vitamins produced by large masses of algae in fresh and marine waters. Vitamins are, therefore, more an extracellular metabolite in Lucas's sense than in Fogg's. Fogg limits the term "extracellular metabolite" to those metabolic products which are secreted into the surrounding milieu by healthy, growing cells—an essential limitation in many studies. Lucas's less stringent definition is more appropriate to this present discussion, since the presence and availability of metabolites, more than the mode of production, is significant to community structure.

As early as 1943 the cycles of thiamine and biotin in lake waters were studied by Hutchinson (in 1946 he and Setlow added niacin). Sufficient quantities of these vitamins were present in the waters studied for the needs of the vitamin-requiring algae. In 1956 Cowey found that the B_{12} in the sea is also present at adequate levels and Droop (1957) confirmed abundant B_{12} in a variety of marine habitats; however, his later work with the B_{12} binding factor (an algal extracellular metabolite) does suggest that ambient levels may not actually represent available levels (1968), and his identification of the phytoplankter Monochrysis lutheri as the producer of the proteinaceous B_{12}-binder makes this binding a type of vitamin-associated antibiosis among phytoplankters.

The biotic origin and utilization of aquatic vitamin stores was confirmed directly in vitro by studies of vitamin production by marine bacteria (Burkholder and Burkholder, 1956; Menzel and Spoehr, 1962) and indirectly in situ by the many observations that concentrations of vitamins in the open sea are generally lower than they are in coastal waters where the greater portion of primary production is localized. Until 1970, however, the source of these marine and freshwater vitamin stores was believed to be either bacterial or terrestrial. It was then that Carlucci and Bowes (1970a, 1970b), by confirming in vitro production of vitamins by several species of marine algae, provided a strong argument for the inclusion of algae among not only the users of, but also the contributors to, the in situ vitamin pool.

The level of vitamins in natural waters is determined by a balance between producers and consumers, and variations in vitamin levels in the sea have been found to correlate with population increases of vitamin-requiring algae. In 1956 Cowey found that a drop in B_{12} concentration coincided with May-June diatom blooms (many diatoms used exogenous B_{12}), and in 1959 Vishniac and Riley observed a drop in B_{12} levels which paralleled a drop in NO_3 during blooms of Skeletonema costatum in Long Island Sound, suggesting a direct correlation between NO_3 utilization in cell growth processes and the consumption of B_{12}. The widespread occurrence of vitamins in measurable quantities in both marine and fresh waters, and the demonstrated capacity of both bacteria and algae to produce, bind, and, or, use these vitamins are clear examples of extracellular metabolite-mediated pro- and antibiosis in situ.

REVIEWS

More than half a century of discussion concerning the relationships between *in situ* measurements of dissolved metabolic products in aquatic ecosystems and their possible pro- or antibiotic activities is recorded in the scientific literature (comprehensive studies and reviews: Lucas, 1947; Lefèvre, *et al*., 1952; Aubert, 1963-1975; Fogg, 1952; 1966; 1971; with Westlake, 1955; Rice, 1954; Saunders, 1957; Hartman, 1960; Pourriot, 1966; Keating 1976; primarily terrestrial: Mölish, 1937; Rice, 1974; including a major section on aquatic allelopathy, 1979).

With the publications of Pratt's detailed work with *Chlorella* in culture (1940, 1942, 1943), Rice's (1954) thorough studies of algal allelopathy as applied to *in situ* events, Droop's work on B_{12} binding (1968), Wetzel's and Allen's work on freshwater macrophytes (Wetzel and Allen, 1971; Allen, 1971, Wetzel, 1969), and of Aubert's extensive studies of the interactions among marine plankton (1963-1975), the *in situ* occurrence and significance of both pro- and antibiosis in aquatic environments was firmly established. Ecologically significant roles for pro- and antibiosis in the development of planktonic community structure in freshwater ecosystems were substantiated by Williams in 1971 with his demonstration of the allelopathic influence which *Anabaena flos-aquae* exercised in its domination of a freshwater plankton community, and by Keating (1977, 1978) with evidence of *in situ* and *in vitro* patterns of phytoplankton pro- and antibiosis controlling bloom sequence and long-term successional changes in the eutrophied waters of Linsley Pond.

What use, then, can we make of this extensive mosaic of plausibly established general patterns of extracellular metabolite involvement in the structuring of a planktonic community? It is counter-productive to maintain the stance of indifference simply because a great deal of additional study is required (both to strengthen those explanations presently offered for the foregoing observations, and to elucidate specific mechanisms of effect for the many pro- and antibiotic effects associated with both extracellular and membrane-bound metabolites).

Cautious exploration of this type of information would allow attempts to be made now to interfere with planktonic populations (biomanipulation) in such ways as might reasonably improve *in situ* conditions.

ONE PLAUSIBLE* INTERFERENCE

During a three-year study of a culturally eutrophied lake in Connecticut (Linsley Pond) some unusually informative patterns of bloom dominance were evident. Each of the three years produced a distinct bloom pattern but certain features were common to all years. Blue-green blooms dominated the plankton community through the entire first year, including the winter months. During this time concentrated populations of blue-greens filled the epilimnion. The anaerobic hypolimnion usually contained viable trichomes (they were amenable to aerobic test tube culture), but concentrations were only a fraction of those in the epilimnion.

In the following summer and fall blue-greens continued to dominate generally; however, a period of blue-green free water occurred in the late winter. This was followed by a brief spring diatom bloom. That diatom bloom was dominated by _Asterionella formosa_, and ended when the _available_** silica was insufficient to support the bloom (Keating, 1978a; 1978b).

With the demise of the diatom bloom in the second spring the blue-green populations took over the plankton community and maintained dominance until fall. In the third winter no blue-green blooms developed in the lake. Waters were, in fact, free of blue-green blooms from September through January at which time a small population of blue-greens accompanied the first signs of a spring diatom bloom. In the spring (1974) an extensive, diverse, diatom bloom dominated the plankton community. As in the prior spring, when available silica could no longer maintain the diatom population, it gave way to a rather dramatic summer bloom of blue-greens. This bloom, however, came much later than that of the prior summer; therefore, more of the excessive nutrient load of these waters had been invested in desirable (from a food chain point of view), eukaryotic, diatoms, and less was left around to encourage blue-greens—the excess macronutrients had been well-invested in fish food. If *in vitro* nutrient addition studies done with Linsley waters taken before and after the diatom bloom reflect the nutrient conditions *in situ* (if Occham's razor is employed, this premise is difficult to ignore), then the simple addition of silica, in an available form, would have extended the period of diatom dominance further into the late summer. This would have invested more of the excess macronutrients in fish food while depriving the blue-greens of those same nutrients.

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*It is somewhat disconcerting to me that this plausible interference has been employed in the last several years in a variety of situations, some of which may not be entirely suited to its application—yet it has never been demonstrated under scientific control in a situation which would be entirely suited to its application.

**available ≠ present.

Certain additional characteristics of the system under scrutiny are important. When blue-greens reach senescence, they lyse and their cellular contents are dumped back into the epilimnion for recycling. When diatoms reach senescence, they sink into the hypolimnion carrying much of their nutrient store with them. In a lake with a well-developed thermocline this effectively removes nutrients from the reach of the plankton community—at least until the next fall turnover. At that time, since winter waters are cold, the capacity of organisms to employ these turnover-released nutrients is less than it would be in the spring or summer.

From a management standpoint there are multiple advantages to encouraging diatom blooms in lieu of blue-green blooms: 1) diatoms employ nutrients once and carry cellular material into the hypolimnion after this single use where it remains until turnover; 2) diatoms are an excellent food source for zooplankters and fish; i.e., they are a desirable inclusion in the food chain; 3) blue-greens lyse in the epilimnion and release most of their cellular material in place, making nutrients available repeatedly for recycling by new blue-green blooms (this exaggerates the already excessive macronutrient load of a culturally eutrophied lake); 4) blue-greens are at least a poor nutritional source; i.e., they are an undesirable inclusion in the food chain; 5) blue-greens are very likely to be producers of extracellular products which function as antibiotics against several more desirable food algae in their own trophic level, and against zooplankters and fishes (and, at times, mammals) in higher trophic levels; i.e., they are a disruptive inclusion in the plankton community; 6) blue-greens are aesthetically offensive; they visibly discolor lake waters; they smell (their odors pervade the air in the vicinity of ailing lakes); and, finally, swimmers are conscious of an odd taste and a "slimy" feeling in blue-green dominated waters (at least they are silent).

It is useful, then, from a management point of view to encourage diatoms at the expense of blue-greens. Actually, it would be useful alone either to encourage diatoms, or to discourage blue-greens, but it is especially desirable to do both at once. This should be possible. The progress of a spring diatom bloom (in a year when there is a spring diatom bloom) should be carefully monitored. When the bloom evidences a plateau (or a rapid change from increasing populations to stable or decreasing populations), silica in a form readily available to diatoms should be added. This should enable the diatoms to maintain their dominance of the plankton community for a longer period. (There are many species of diatom *in situ*. Surely, not all are limited by specific day lengths, or precise temperature regimes. Any species of diatom which can be encouraged by silica addition is to be preferred to blue-greens.) The application of silica to lake waters (in the form of commercial grade sodium silicate, water glass, as is included in common cement) could be accomplished in precisely the same rather unsophisticated (but quite functional) manner as the application of $CuSO_4$; i.e., it can be placed in a canvas sack, and the sack can then be dragged around in the lake by a boat equipped with a pair of oars and a strong back. Sodium silicate does not long remain soluble, but controlled applications, placed directly into diatom-filled waters, should be readily taken in by those diatoms. It might be productive to reapply the silica treatment several times during the critical period; however, sooner or later some other nutrient would interfere with diatom growth. This will not occur immediately—remember we are dealing only with lakes bearing excessive nutrient loads. Remember, too, that every molecule of macronutrient invested in diatom growth is one less invested in blue-green growth. At present the level of application and the number of applications should be very carefully determined for every lake system. If some general application factor is developed as a result of information and understanding gained during initial demonstration projects (which should include excessive; i.e., very conservative, controls), then more flexibility and generalization could be allowed.

It is anticipated that adding sodium silicate would raise the pH of lake waters. No other general effects are known to me. Many additional effects must be anticipated—some may be harmful. In the few tests we have done with catfish sensitivity to sodium silicate no harm was evident when stepwise additions of sodium silicate were increased until concentrations passed the point of precipitation. Precipitation did cause considerable distress to catfish—after 24 hours of exposure two out of four died. The other two survived in fish tanks (minus the excess silica) for more than two years. The need for very careful application of these suggestions under very carefully monitored circumstances with a maximum of scientific control is essential (the basis for the concern expressed at the beginning of this section).

The question as to why this particular discussion should be included in a rather long review of extracellular metabolite involvement in plankton community structure must have entered the reader's thoughts by now. There is, I hope, an enlightening answer available. The alternation of blue-green and diatom blooms is fairly obvious in the bloom pattern of Linsley Pond. If there are no spring diatom blooms, there can be no value to encouraging what is not there in the first place. It would, however, be quite useful in such situations if we could insert a spring diatom bloom in those years when one did not occur under its own steam.* This is the point at which the foregoing discussion of management tactics relates to extracellular metabolite effects. Blue-greens produce extracellular products (leaked or lysis-released). These products remain behind after blue-green cells are gone and interfere with the growth of diatoms (40 plus taxa, including three marine taxa, were tested against cell-free filtrates of 10 blue-green cultures, Keating, 1977; 1978a; 1978b). If winter waters are dominated by high concentrations of blue-greens (at least in Linsley), they seem to prevent the diatoms in the following spring from reaching their maximum possible population potentials. If the blue-greens were eliminated (preferably in the late fall, or early winter, immediately after fall turnover), the diatom-interfering extracellular products which were left behind would be (sufficiently) neutralized in situ by bacterial degradation and dispersion in a period of four weeks (estimate based on observations from the aforereferenced study). If a blue-green bloom were intentionally copper-sulfated out of existence in the early winter, the cold winter waters would not allow the rapid return of a new blue-green population (my observation has been that it takes two to three weeks for a new blue-green bloom to replace a copper-sulfated blue-green bloom in the summer). Once cleared, winter waters would purge themselves of the interfering blue-green metabolites allowing a diatom bloom in the early spring. This suggests that the 1971-1972 winter phytoplankton pattern (Figure 1) could be changed so as to match the 1973-1974 winter pattern. Thereafter, the addition of silica might allow a diatom bloom such as that evidenced in 1974 to be extended a bit longer into the summer, pushing the blue-green bloom of Oscillatoria rubescens (535) further into the late summer or early fall (a less than perfect set of conditions—but a genuine improvement in that the period of diatom dominance is extended at the expense of the period of blue-green dominance). Under the conditions evidenced in the summer of 1974 the entire trophic structure of the lake community would be healthier than it would be under the conditions of the summer of 1972. For example bluegills were abundant in the summer of 1974, yet none were observed during the summer of 1972. They apparently survived the deprivation of the blue-green dominated years, but in greatly reduced numbers.

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*The philosophical view that we should not pervert natural sequences is respected by this author, but cultural eutrophication is an accomplished perversion of natural sequences, and at worst, we are continuing an intrusion—at best we are returning the system to a more "natural" sequence.

It was suggested (Keating, 1976) that the management tactics involving $CuSO_4$-elimination of fall/winter blue-green blooms and silica-encouragement of spring/summer diatom blooms be explored both to determine if they were as innocuous as they seemed, and to determine if they would produce the plausible desired improvements in a culturally eutrophied lake. The suggestion was taken a bit too enthusiastically by some, and a number of lakes, not chosen for the characteristics most likely to provide a clear-cut, controlled demonstration; i.e., strong thermocline development, obvious blue-green winter dominance, were targeted for this type of treatment. Since experience under carefully selected, well-monitored conditions might ultimately have indicated that the concept is damaging in ecological terms, or is simply impractical, controlled demonstration should have preceded general application. Fortunately, no horror stories have yet surfaced relating to these somewhat premature applications. Still, a highly controlled demonstration might allow refinement and improvement of what is really only a set of promising management tactics, and this might ultimately increase our general capacity to improve conditions in culturally eutrophied lakes when nutrient removal or diversion is unrealistic or impractical. A very carefully planned demonstration project is still needed.

REFERENCES

Aaronson, S. 1978. Excretion of organic matter by a phytoplankton in vitro. LIMNOLOGY AND OCEANOGRAPHY 23:838.

Akehurst, S.C. 1931. Observations on pond life, with special reference to the possible causation of swarming of phytoplankton. JOURNAL OF THE ROYAL MICROSCOPICAL SOCIETY 51:237-261.

Aleyev, B. 1934. Secretions of organic substances by algae into the surrounding medium. MIKROBIOLOGIA (Moscow) 3:506-508.

Allee, W. 1934. Recent studies in mass physiology. BIOLOGICAL REVIEW 9:1-48.

Allen, E. 1922. (Cited in Akehurst, 1931) Source publication unknown.

Allen, H.L. 1971. Primary productivity, chemo-organotrophy and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. ECOLOGICAL MONOGRAPHS 41:97-127.

Anderson, G.C.; Comita, G.W., and V. Engstrom-Heg. 1955. A note on the phytoplankton-zooplankton relationships in two lakes in Washington. ECOLOGY 36:757-759.

Antia, N.; McAllister, C.; Parsons, T.; Stephens, K. and J. Strickland. 1963. Further measurement of primary production using a large-volume plastic sphere. LIMNOLOGY AND OCEANOGRAPHY 8:166-183.

Arnold, D.E. 1971. Ingestion, assimilation, survival and reproduction by Daphnia pulex fed seven species of blue-green algae. LIMNOLOGY AND OCEANOGRAPHY 16:906-920.

Aubert, M. 1963-1975. REVUE INTERNATIONALE D'OCÉANOGRAPHIE MÉDICALE. (An extensive series of articles by this author and colleagues in this journal).

Aziz, K. 1974. Diarrhea toxin obtained from a waterbloom-producing species, Microcystis aeruginosa, Kützing. SCIENCE 183:1206-1207.

Bentley, J. 1958. Role of plant hormones in algal metabolism and ecology. NATURE 181:1499-1502.

Bentley-Mowat, J. and S.M. Reid. 1969. Effect of gibberellins, kinetin and other factors on the growth of unicellular marine algae in culture. BOTANICA MARINA 7:185-199.

Berland, B.; Bonin, D.; Cornu, A.; Maestrini, S. and J. Marine. 1972. The antibacterial substances of the marine algae Stichochrysis immobilis (Chrysophytyta). JOURNAL OF PHYCOLOGY 8:383-392.

Berman, M.S. and S. Richman. 1974. The feeding behavior of Daphnia pulex from Lake Winnebago, Wisconsin. LIMNOLOGY AND OCEANOGRAPHY 19:105-109.

Braarud, T. and B. Føyn. 1930. Beiträge zur Kenntnis des Stoffwechsels im Meere. AVHANDLUNGEN NORSKE VIDENSKAPS AKADEMI (Oslo) 14:1-24.

Broom, J. 1929. (Cited in Akehurst, 1931) Source publication unknown.

Burkholder, P. and L. Burkholder. 1956. Vitamin-producing bacteria in the sea. INTERNATIONAL OCEANOGRAPHIC CONGRESS, PREPRINTS, AAAS 912-913.

Burns, C.W. 1968a. Direct observations of mechanisms regulating feeding behavior of *Daphnia* in lake water. INTERNATIONALE REVUE DER GESAMTE HYDROBIOLOGIE 53:83-100.

Burns, C.W. 1968b. The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. LIMNOLOGY AND OCEANOGRAPHY 13:675-678.

Burns, C.W. and F.H. Rigler. 1967. Comparison of filtering rates of *Daphnia rosea* in lake water and in suspensions of yeast. LIMNOLOGY AND OCEANOGRAPHY 12:492-502.

Carlucci, A. and P. Bowes. 1972. Vitamin B_{12}, thiamine and biotin contents of marine phytoplankton. JOURNAL OF PHYCOLOGY 8:133-137.

Carlucci, A. and P. Bowes. 1970a. Production of vitamine B_{12}, thiamine and biotin by phytoplankton. JOURNAL OF PHYCOLOGY 6:351-357.

Carlucci, A. and P. Bowes. 1970b. Vitamin production and utilization by phytoplankton in mixed culture. JOURNAL OF PHYCOLOGY 6:393-400.

Cowey, C. 1956. A preliminary investigation of the variations of vitamin B_{12} in oceanic and coastal waters. JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION, UNITED KINGDOM 35:609-620.

Cowles, H.C. 1911. The causes of vegetative cycles. BOTANICAL GAZETTE (Chicago) 51:161-183.

Cruickshank, I.A. and D.R. Perrin. 1964. Pathological function of phenolic compounds in plants. BIOCHEMISTRY OF PHENOLIC COMPOUNDS (J.B. Harborne, ed.) 511-544.

Davis, E. and E. Gloyna. 1970. Bactericidal effects of algae on enteric organisms (monograph). x and 132 pp. WATER POLLUTION CONTROL RESEARCH SERIES 18050DOL 03/70, UNITED STATES GOVERNMENT PRINTING OFFICE.

Denffer, D. 1948. Über einen Wachstumshemmstoff in alternden Diatomeenkulturen. BIOLOGISCHES ZENTRALBLATT 67:7-13.

Droop, M. 1968. Vitamin B_{12} and marine ecology. IV. The kinetics of uptake, growth and inhibition in *Monochrysis lutheri*. JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION 48:689-733.

Droop, M. 1957. Vitamin B_{12} in marine ecology. NATURE 180:1041-1042.

Duff, D.; Bruce, D. and N. Antia. 1966. The antibacterial activity of marine planktonic algae. CANADIAN JOURNAL OF MICROBIOLOGY 12:877-884.

Edmondson, W.T. 1965. Reproductive rate of planktonic rotifers as related to food and temperature in nature. ECOLOGICAL MONOGRAPHS 35:61-111.

Edmondson, W.T. 1957. Trophic relations of the zooplankton. TRANSACTIONS OF THE AMERICAN MICROSCOPICAL SOCIETY 76:225-246.

Fitzgerald, G. 1969. Some factors in the competition or antagonism among bacteria, algae, and aquatic weeds. JOURNAL OF PHYCOLOGY 5:351-359.

Fitzgerald, G.P. 1964. The biotic relations within water blooms. ALGAE AND MAN (D. Jackson, ed.) 300-306.

Flint, L. and F. Moreland. 1946. Antibiosis in the blue-green algae. AMERICAN JOURNAL OF BOTANY 33:218 (abstract).

Fogg, G.E. 1977. Excretion of organic matter by phytoplankton. LIMNOLOGY AND OCEANOGRAPHY 22:576-577.

Fogg, G.E. 1971. Extracellular products of algae in freshwater. ARCHIVES FOR HYDROBIOLOGY 5:1-25.

Fogg, G.E. 1966. The extracellular products of algae. OCEANOGRAPHIC AND MARINE BIOLOGY ANNUAL REVIEW (H. Barnes, ed.) 4:195-212.

Fogg, G.E. 1962. Extracellular products. PHYSIOLOGY AND BIOCHEMISTRY OF ALGAE (R. Lewin, ed.) 475-489.

Fogg, G.E. 1952. The production of extracellular nitrogenous substances by a blue-green algae. PROCEEDINGS OF THE ROYAL SOCIETY OF LONDON (Series B) 139:372-397.

Fogg, G.E. 1953. THE METABOLISM OF ALGAE. London: Methuen and Company, Limited. ix and 149.

Fogg, G.E. and D.F. Westlake. 1955. The importance of extracellular products of algae in freshwater. VERHANDLUNGEN INTERNATIONALE VEREINIGUNG FÜR THEORETISCHE UND ANGEWANDTE LIMNOLOGIE 12:219-232.

Friedman, M. and J.R. Strickler. 1975. Chemoreceptors and feeding in calanoid copepods (Arthropoda: Crustacea). PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES. 72:4185-4188.

Gause, G.; Nastukova, O. and W. Alpatov. 1934. The influence of biologically conditioned media on the growth of a mixed population of *Paramecium caudatum* and *P. aurelia*. JOURNAL OF ANIMAL ECOLOGY 3:222-230.

Gibor, A. 1956. Some ecological relationships between phyto- and zooplankton. BIOLOGICAL BULLETIN 111:230-234.

Gilbert, P. 1974. (Interview). "Red Tide" hinders professor's research. CORNELL REPORTS. 8:pages 1 and 7.

Gorham, P. 1964. Toxic algae. ALGAE AND MAN (D. Jackson, ed.) 307-336.

Harder, R. 1917. Ernährungsphysiologische Untersuchungen an Cyanophyceen, hauptsächlich dem endophytischen Nostoc punctiforme. ZEITSCHRIFT FÜR BOTANIK (Z. FÜR PFLANZENPHYSIOLOGIE) 9:145-242.

Hardy, A.C. 1936a. Plankton ecology and the hypothesis of animal exclusion. PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON (Part II) 148:64-70.

Hardy, A.C. 1936b. The ecological relations between the herring and the plankton investigated with the plankton indicator. JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION, UNITED KINGDOM 21:147-177.

Hardy, A.C. and E.R. Gunther. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926-1927. DISCOVERY REPORTS 11:1-456.

Hartman, R. 1960. Algae and metabolites of natural waters. THE ECOLOGY OF ALGAE: PYMATUNING SYMPOSIA IN ECOLOGY (Tryon and R. Hartman, eds.) 2:38-55.

Harvey, H.W. 1945. RECENT ADVANCES IN THE CHEMISTRY AND BIOLOGY OF SEA WATER. Cambridge University Press, U.K. 164 pp.

Harvey, H.W.; Cooper, L.H.N.; Lebour, M.V. and F.S. Russell. 1935. Plankton production and its control. JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION, UNITED KINGDOM 20:407-422.

Heinle, D.R. 1969. Culture of Calanoid Copepods in synthetic sea water. JOURNAL FISHERIES RESEARCH BOARD OF CANADA 26:150-153.

Hellebust, J. 1965. Excretion of some organic compounds by marine phytoplankton. LIMNOLOGY AND OCEANOGRAPHY 10:192-206.

Hutchinson, G.E. 1967. A TREATISE ON LIMNOLOGY. Volume II. INTRODUCTION TO LAKE BIOLOGY AND THE LIMNOPLANKTON. John Wiley and Sons, Inc.; New York, London, Sydney. xi and 1115.

Hutchinson, G.E. 1961. The paradox of the plankton. AMERICAN NATURALIST 95:137-145.

Hutchinson, G.E. 1944. Limnological studies in Connecticut VII: A critical examination of the supposed relationship between phytoplankton periodicity and chemical changes in lake waters. ECOLOGY 25:3-26.

Hutchinson, G.E. 1943. Thiamine in lake waters and aquatic organisms. ARCHIVES OF BIOCHEMISTRY 2:143-150.

Hutchinson, G.E. and J. Setlow. 1946. Limnological Studies in Connecticut. VIII: The niacin cycle in a small inland lake. ECOLOGY 27:13-22.

Ignatiades, L. and G.E. Fogg. 1973. Studies on the factors affecting the release of organic matter by *Skeletonema costatum* (Greville) Cleve in culture. JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION, UNITED KINGDOM. 53:937-956.

Johnston, W. 1933. Effects of population density on the rate of reproduction in *Oxytricha*. PHYSIOLOGICAL ZOOLOGY 6:22-54.

Johnstone, J.; Scott, A. and H. Chadwick. 1924. MARINE PLANKTON. Liverpool University Press, Liverpool.

Jones, G. 1959. Biologically active organic substances in sea water. PREPRINTS INTERNATIONAL OCEANOGRAPHIC CONGRESS 1959 AAAS (M. Sears, ed.) 921-922.

Jørgensen, E. 1962. Antibiotic substances from cells and culture solutions of unicellular algae with special reference to some chlorophyll derivatives. PHYSIOLOGIA PLANTARUM 15:530-545.

Jørgensen, E. 1956. Growth inhibiting substances formed by algae. PHYSIOLOGIA PLANTARUM 9:712-726.

Jørgensen, E. and E. Steeman-Nielsen. 1961. Effect of filtrates from cultures of unicellular algae on the growth of *Staphylococcus aureus*. PHYSIOLOGIA PLANTARUM 14:896-908.

Jørgensen, E. and E. Steeman-Nielsen. 1959. Effects of filtrates from cultures of unicellular algae on the growth of *Staphylococcus aureus*. PREPRINTS INTERNATIONAL OCEANOGRAPHIC CONGRESS AAAS (M. Sears, ed.) 923.

Keating, K.I. 1978a. Blue-green algal inhibition of diatom growth in culture and *in situ*: Transition from mesotrophic to eutrophic community structure. SCIENCE 199:971-973.

Keating, K.I. 1978b. Role of silica availability in blue-green inhibition of diatom growth in eutrophied waters. Abstract for AAAS Meeting, Washington, D.C.

Keating, K.I. 1977. Allelopathic influence on blue-green bloom sequence in a eutrophied lake. SCIENCE 196:885-887.

Keating, K.I. 1976. ALGAL METABOLITE INFLUENCE ON BLOOM SEQUENCE IN EUTROPHIED FRESHWATER PONDS EPA-600/3-76-081, Ecological Research Series.

Kroes, H. 1971. Growth interactions between *Chlamydomonas globosa* Snow and *Chlorococcum ellipsoideum* Deason and Bold under different experimental conditions with special attention to the role of pH. LIMNOLOGY AND OCEANOGRAPHY 16:869-879.

Kroes, H. 1972. Growth interactions between *Chlamydomonas globosa* Snow and *Chlorococcum ellipsoideum* Deason and Bold: The role of extracellular products. LIMNOLOGY AND OCEANOGRAPHY 17:423-432.

Krogh, A. and E. Lange. 1930. On the organic matter given off by algae. BIOCHEMICAL JOURNAL 24:1666-1671.

Krueger, D. 1980 (in press). Embryological induction and ecology of *Daphnia pulex*.

Lefèvre, M. 1964. Extracellular products of algae. ALGAE AND MAN (D. Jackson, ed.) 337-367.

Lefèvre, M. 1950. *Aphanizomenon gracile*, Lemm. cyanophyte defavorable au zooplankton. ANNALS DE LA STATION CENTRALE D'HYDROBIOLOGIE APPLIQUÉE 3:205-208.

Lefèvre, M.; Jakob, H. and M. Nisbet. 1952. Auto, et hétéroantagonisme chez les algues d'eau douce *in vitro* et dans les collections d'eau naturelles. ANNALS DE LA STATION CENTRALE D'HYDROBIOLOGIE APPLIQUÉE 4:1-197.

Lefèvre, M. and M. Nisbet. 1948. Sur la sécrétion, par certaines espèces de'Algues de substances inhibitrices d'autres espèces d'Algues. COMPTES RENDUS 226:107-109.

Levring, T. 1945. Some culture experiments with marine plankton diatoms. MED. OCEANOGRAPHIC INSTITUTE GÖTEBORG 3(12).

Lewin, R. 1956. Extracellular polysaccharides of green algae. CANADIAN JOURNAL OF MICROBIOLOGY 2:665-672.

LoCicero, V.R. (ed.). 1975. PROCEEDINGS OF THE FIRST INTERNATIONAL CONFERENCE ON TOXIC DINOFLAGELLATE BLOOMS. Massachusetts Science and Technology Foundation, Wakefield, Mass. viii and 541.

Lucas, C.E. 1947. The ecological effects of external metabolites. BIOLOGICAL REVIEWS 22:270-295.

Mast, S. and D. Pace. 1938. The effect of substances produced by *Chilomonas paramecium* on rate of reproduction. PHYSIOLOGICAL ZOOLOGY 11:359-382.

McLachlan, J. and J. Craigie. 1964. Algal inhibition by yellow ultraviolet-absorbing substances from *Fucus vesiculosus*. CANADIAN JOURNAL OF BOTANY 42:287-292.

McMahon, J.W. and F.H. Rigler. 1965. Feeding rate of *Daphnia magna* Straus in different foods labeled with radioactive phosphorus. LIMNOLOGY AND OCEANOGRAPHY 10:105-114.

McMahon, J.W. and F.H. Rigler. 1963. Mechanisms regulating the feeding rate of *Daphnia magna* Straus. CANADIAN JOURNAL OF ZOOLOGY 41:321-332.

Menzel, D. and J. Spoehr. 1962. Occurrence of vitamin B_{12} in the Sargasso Sea. LIMNOLOGY AND OCEANOGRAPHY 7:151-154.

Moebus, K. 1972a. Seasonal changes in antibacterial activity of North Sea Water. MARINE BIOLOGY 13:1-13.

Moebus, K. 1972b. The influence of storage on anti-bacterial activity of sea water. I. Experiments with sea water stored at 18°C. MARINE BIOLOGY 13:346-351.

Moebus, K. 1972c. Bacteriocidal properties of natural and synthetic sea water as influenced by addition of low amounts of organic matter. MARINE BIOLOGY 15:81-88.

Mölish, H. 1937. DER EINFLUSS EINER PFLANZE AUF DIE ANDERE - ALLELOPATHIE. Fischer Verlag, Jena.

Mullin, M.M. 1963. Some factors affecting the feeding of marine Copepods of the genus Calanus. LIMNOLOGY AND OCEANOGRAPHY 8:239-250.

Murphy, D.W.; Sohi, S.S., and P.G. Fast. 1976. Bacillus thuringiensis enzyme-digested delta endotoxin: Effect on cultured insect cells. SCIENCE 194:954-956.

Myers, J. and J. Johnston. 1949. Carbon and nitrogen balance of Chlorella during growth. PLANT PHYSIOLOGY 24:111-119.

Nalewajko, C. 1966. Photosynthesis and excretion in various planktonic algae. LIMNOLOGY AND OCEANOGRAPHY 11:1-10.

Naumann, E. 1923. Spezielle Untersuchungen über die Ernährungsbiologie des tierischen Limnoplanktons. II. Über den Nahrungserwerb und die naturliche Nahrung der Copepoden und die Rotiferen des Limnoplanktons. LUNDS UNIVERSITÄT ARSSK n.f. 19:3-17.

Naumann, E. 1921. Spezielle Untersuchungen über die Ernährungsbiologie des tierischen Limnoplanktons. I. Über die Technik des Nahrungserwerbs bei den Cladoceran und ihre Bedentung für die Biologie der Gewässertypen. LUNDS UNIVERSITÄT ARSSK n.f. 17:3-26.

Naumann, E. 1918. Uber die naturliche Nahrung des limnischen zooplanktons. Ein Beitrag zur Kenntnis des Stoffhaushalts in Susswasser. LUNDS UNIVERSITAT ARSSK n.f. 14:1-48.

Parker, B.C. and H.C. Bold. 1961. Biotic relationships between soil algae and other microorganisms. Am. J. Bot. 48:185-197.

Pearsall, W. 1932. Phytoplankton in the English lakes II: The composition of the phytoplankton in relation to dissolved substances. JOURNAL OF ECOLOGY 20:241-262.

Pearsall, W. 1923. A theory of diatom periodicity. JOURNAL OF ECOLOGY 11:165-183.

Pennak, R.W. 1946. The dynamics of fresh-water plankton populations. ECOLOGICAL MONOGRAPHS 16:339-355.

Phelps, A. 1935 Growth of protozoa in pure culture. I. Effect upon the growth curve of the age of the inoculum. JOURNAL OF EXPERIMENTAL ZOOLOGY 70:109-130.

Phelps, A. 1936. Growth of protozoa in pure culture. II. Effects upon the growth curve of different concentrations of nutrient materials. JOURNAL OF EXPERIMENTAL ZOOLOGY 72:479-496.

Porter, K.G. 1980 (in press). Nutritional adequacy, manageability, and toxicity as factors that determine the food quality of green and blue-green algae for *Daphnia*. SPECIAL SYMPOSIUM III AMERICAN SOCIETY FOR LIMNOLOGY AND OCEANOGRAPHY.

Porter, K.G. 1976. Enhancement of algal growth and productivity by grazing zooplankton. SCIENCE 192:1332-1334.

Pourriot, R. 1966. Metabolites externes et interactions biochemiques chez les organisms aquatiques. ANNÉE BIOLOGIQUE 7-8:337-374.

Pratt, R. 1943. Studies on *Chlorella vulgaris*. VI. Retardation of photosynthesis by a growth inhibiting substance from *Chorella vulgaris*. AMERICAN JOURNAL OF BOTANY 30:32-33.

Pratt, R. 1942. Studies on *Chlorella vulgaris*. V. Some properties of the growth inhibitor formed by *Chlorella* cells. AMERICAN JOURNAL OF BOTANY 29:142-148.

Pratt, R. 1940. Influence of the size of the inoculum on the growth of *Chlorella vulgaris* in freshly prepared culture medium. AMERICAN JOURNAL OF BOTANY 27:52-56.

Pratt, R. and Fong, J. 1940. Studies on *Chlorella vulgaris*. II. Further evidence that *Chlorella* cells form a growth inhibiting substance. AMERICAN JOURNAL OF BOTANY 27:431-436.

Provasoli, L. 1963. Growing Marine Seaweeds. PROCEEDINGS OF THE 4th INTERNATIONAL SEAWEED SYMPOSIUM. 9-17.

Putter, A. 1908. Der Stoff haushalt des Meeres. ZEITCHRIFT DER ALLGEMEIN-DER PHYSIOLOGIE 7:321-368.

Quick, J. 1973. Fish malady blamed on green algae. NEW HAVEN REGISTER, March 24, 1973.

Ransom, R.; Nerad, T. and P. Meier. 1978. Acute toxicity of some blue-green algae to the protozoan *Paramecium caudatum*. JOURNAL OF PHYCOLOGY 14:114-116.

Rice, E.L. 1979. Allelopathy—An Update. THE BOTANICAL REVIEW. 45:15=-109.

Rice, E.L. 1974. ALLELOPATHY. Academic Press, New York, San Francisco, and London. x and 353.

Rice, T.R. 1954. Biotic influences affecting population growth of planktonic algae. FISHERY BULLETIN 87 from FISHERY BULLETIN OF THE FISH AND WILDLIFE SERVICE (USGPO) 54:227-245.

Richman, S.; Smayda, T. and M. Melnik. 1980. Direct observations of *Daphnia* mouth part responses to algal food compositions of varying quality. ANNUAL MEETING AMERICAN SOCIETY OF LIMNOLOGY AND OCEANOGRAPHY. June 16-19.

Rigler, F.H. 1961. The relation between concentration of food and feeding rate of *Daphnia magna* Straus. CANADIAN JOURNAL OF ZOOLOGY 39:857-868.

Riley, G.A. 1940. Limnological studies in Connecticut. Part III. The plankton of Linsley Pond. ECOLOGICAL MONOGRAPHS 10:279-306.

Robbins, W.; Hervey, A. and M. Stebbins. 1951. Further observations on *Euglena* and B_{12}. BULLETIN OF THE TORREY BOTANICAL CLUB 78:363-375.

Robertson, T. 1921a. Experimental studies on cellular multiplication. I. The multiplication of isolated infusoria. BIOCHEMICAL JOURNAL 15:595-611.

Robertson, T. 1921b. Experimental studies on cellular multiplication. II. The influence of mutual contiguity upon reproductive rate and the part played therein by the "X-substance" in bacterised infusions which stimulates the multiplication of infusoria. BIOCHEMICAL JOURNAL 15:612-619.

Ryther, J.H. 1954. Inhibitory effects of phytoplankton upon the feeding of *Daphnia magna* with reference to growth, reproduction, and survival. ECOLOGY 35:522-533.

Saunders, G.W. 1957. Interrelations of dissolved organic matter and phytoplankton. BOTANICAL REVIEW 23:389-409.

Saz, A.; Watson, G.; Brown, S. and D. Lowery. 1963. Antimicrobial activity of marine waters. I: Macromolecular nature of anti-staphylococcal factor. LIMNOLOGY AND OCEANOGRAPHY 8:63-67.

Schindler, J.E. 1971. Food quality and zooplankton nutrition. JOURNAL OF ANIMAL ECOLOGY 40:589-595.

Schindler, D.W. 1968. Feeding, assimilation, and respiratory rates of *Daphnia magna* under various environmental conditions and their relation to production estimates. JOURNAL OF ANIMAL ECOLOGY 37:369-385.

Schopf, J.W. 1980. Press release June 19, 1980. N.Y. TIMES. Fossils in ancient Australian rock found to be oldest biological cells (R. Reinhold). Pages 1 and 19 (Section A).

Schwimmer, D. and M. Schwimmer. 1964. Algae and medicine. ALGAE AND MAN (D. Jackson. ed.) 368-412.

Shapiro. J. 1980. *Aphanizomenon flos-aquae*—is it stimulated chemically by *Daphnia* to form inedible colonies. Abstract for ANNUAL MEETING AMERICAN SOCIETY OF LIMNOLOGY AND OCEANOGRAPHY, June 16-19.

Sharp, J.H. 1978. Reply to comment by S. Aaronson. LIMNOLOGY AND OCEANOGRAPHY 23:839-840.

Sharp, J.H. 1977. Excretion of organic matter by marine phytoplankton: Do healthy cells do it? LIMNOLOGY AND OCEANOGRAPHY 22:381-399.

Sieberth, J. 1964. Role of algae in controlling bacterial populations in estuarine waters. INTERNATIONAL COMMITTEE FOR SCIENTIFIC EXPLORATION OF THE MEDITERRANEAN SEA. 217-233.

Sládeček, V. 1958. A note on the phytoplankton-zooplankton relationship. ECOLOGY 39:547-549.

Sorokin, J.I. 1968. The use of ^{14}C in the study of the nutrition of aquatic animals. MITTEILUNGEN INTERNATIONALE VEREINIGUNG FÜR THEORETISCHE UND ANGEWANDTE LIMNOLOGIE No. 16, 41 p.

Stangenberg, M. 1968. Toxic effects of *Microcystis aeruginosa*, Kg. extracts on *Daphnia longispina*, O.F. Muller and *Eucypris virens*, Jurine. HYDROBIOLOGIA 32:81-87.

Steeman-Nielsen, E. 1955. An effect of antibiosis produced by plankton algae. NATURE 448:553.

Steeman-Nielsen, E. 1934. Dana Report #4.

Stewart, W.D.P. (ed.). 1974. ALGAL PHYSIOLOGY AND BIOCHEMISTRY. University of California Press, Berkeley and Los Angeles. xi and 989.

Stickney, J.S. and P.R. Hoy. 1881. Toxic action of black walnut. TRANSACTIONS OF THE WISCONSIN STATE HORTICULTURAL SOCIETY 11:166-167.

Stross, R.G. 1975. Zooplankton reproduction and water blooms. BIOASSAY TECHNIQUES AND ENVIRONMENTAL CHEMISTRY 467-478.

Talling, J. 1957. The growth of two plankton diatoms in mixed cultures. PHYSIOLOGIA PLANTARUM 10:215-223.

Taub, F. and F. Dollar. 1964. The nutritional inadequacy of *Chlorella* and *Chlamydomonas* as food for *Daphnia pulex*. LIMNOLOGY AND OCEANOGRAPHY 9:61-74.

Vishniac, H. and G. Riley. 1959. B_{12} and thiamine in Long Island Sound: pattern of distribution and ecological significance. PREPRINTS AAAS INTERNATIONAL OCEANOGRAPHY CONGRESS (M. Sears, ed.) 942-943.

Wetzel, R. 1969. Excretion of dissolved inorganic compounds by aquatic macrophytes. BIOSCIENCE 19:539-540.

Wetzel, R. and H. Allen. 1971. Functions and interactions of dissolved organic matter and the littoral zone in lake metabolism and eutrophication. PRODUCTIVITY PROBLEMS OF FRESHWATERS (Z. Kajak and A. Hillbricht-Ilkowska, eds.).

Whittaker, R.H. and P.P. Feeney. 1977. Allelochemics: Chemical interactions between species. SCIENCE 171:757-770.

Whitton, B. 1965. Extracellular products of blue-green algae. JOURNAL OF MICROBIOLOGY 40:1-11.

Williams, L. 1971. The role of heteroinhibition in the development of Anabaena flos-aquae waterblooms. Dissertation, Rutgers University.

Wimpenny, R.S. 1973. The size of diatoms. V. The effect of animal grazing. JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION 53:957-974.

Woodruff, L. 1913. The effect of excretion products of infusoria on the same, and on different, species with special reference to the protozoan sequence in infusions. JOURNAL OF EXPERIMENTAL ZOOLOGY 14:575-582.

Wright, J.C. 1958. The limnology of Canyon Ferry Reservoir. I. Phytoplankton-zooplankton relationships in the euphotic zone during September and October 1956. LIMNOLOGY AND OCEANOGRAPHY 3:150-159.

CYANOPHAGES--ARE THEY POTENTIAL BIOLOGICAL CONTROL AGENTS OF NUISANCE BLUE-GREEN ALGAE?

Paul R. Desjardins
Department of Plant Pathology, University of
California, Riverside, CA 92521

INTRODUCTION

Krauss (1961) and Fogg (1969) pointed out sometime ago that the increased eutrophication of bodies of fresh water often results from man's disturbance of the ecological balance in nature. They also indicated that the development of nuisance levels of certain blue-green algal species in such water bodies is merely a symptom of this increased eutrophication. Nuisance levels of blue-green algae (blooms) can also increase the eutrophic state of water bodies by increasing the concentration of organic matter when the blooms decay (Lin, 1972) and by the production of extracellular polysaccharides (Sangar and Dugan, 1972).

Before any cyanophage had been discovered, Krauss (1961) predicted they would be found and based his prediction on the sudden collapse of algal blooms when nutrient levels and environmental conditions were still ideal for continued algal growth. Not too long after Krauss' prediction Safferman and Morris (1963) reported the discovery of the first blue-green algal virus (cyanophage or phycovirus). Subsequent to their report several different viruses or virus strains have been reported infecting both unicellular and filamentous blue-green algae (Brown, 1972; Daft *et al*., 1970; Granhall, 1972; Kosyakov, 1977; Padan and Shilo, 1973; Safferman *et al*., 1969; Safferman *et al*., 1972; Safferman, 1973b;Sherman and Brown, 1978).

Several workers researching cyanophages believe cyanophages are playing a role in the ecology of blue-green algae (cyanobacteria) and that they are affecting natural control of algal blooms and populations in natural waters (Brown, 1972; Cannon, 1975; Granhall, 1972; Krauss, 1961; Jenifer et al., 1974; Lin, 1972; Safferman, 1968 and 1973b;Safferman and Morris, 1964 and 1967; Shane, 1971; Shane et al., 1972; Shilo, 1969, 1971 and 1972). Some of these workers also believe that the lytic cyanophages have the potential for biological control of nuisance species when introduced by man (Brown, 1972; Jackson and Sladecek, 1970; Safferman and Morris, 1964 and 1967; Shane, 1971; Shilo, 1969 and 1972). Safferman and Morris (1964) were the first to suggest this possibility, and they pointed out that the ultimate objective should be to utilize an approach that would replace nuisance species with more desirable species without annihilation of the total algal population. They also pointed out that although many of the newer algicidal agents are somewhat selective, none have been widely accepted. It is known that blue-green algae vary in their sensitivity to the commonly used algicide, copper sulfate (Palmer, 1977). Because of their high specificity the cyanophages would appear to be ideal as algicidal agents. Other properties of cyanophages which recommend them as "the ideal algicide" are listed in Figure 1.

In this paper a brief description will be presented on the methods that have been successfully used to isolate and purify a few of the well characterized cyanophages, and brief descriptions of their morphology and their mode of interaction with their hosts will also be presented. In addition an attempt will be made to delineate some of the problems which may be important in the use of these lytic agents for biological control. Those research needs and priorities that the author considers to be most urgent will also be presented.

For a comprehensive listing of the literature covering cyanophages the reader is referred to the "Practical Directory to Phycovirus Literature" compiled by Safferman and Rohr (1979).

Cyanophages - As an "Ideal Algicide"

Selective and specific for the nuisance

Nontoxic to other microorganisms in food chain

Harmless to man and animals

Incorporated into the cycling of natural elements

No direct effect on water quality

Harmless to mechanical equipment

Increase during use rather than decrease

Figure 1. Properties of cyanophages which recommend them as an ideal algicide

CHARACTERIZED CYANOPHAGES

Since the blue-green algal hosts (cyanobacteria) of the cyanophages are closely related to other bacteria, it is probably not surprising that the cyanophages are similar in morphology and mode of interaction with their hosts to many of the phages infecting bacterial hosts.

ISOLATION. The isolation of cyanophages from natural water samples requires an enrichment step or concentration step or both followed by clarification steps and further enrichment (Safferman, 1968; Safferman, 1973a; Shilo, 1971; Desjardins et al., 1978). Safferman (1968) recommended enrichment (by incubation with a spectrum of algal hosts) followed by clarification by centrifugation and chloroform treatment. Shilo (1971) recommended an initial filtration step followed by concentration by dialysis against polyethylene glycol (PEG MW-20,000) containing magnesium saline. The concentrate is dialyzed against magnesium saline and then subjected to ultrafiltration. The filtrate is then both assayed for cyanophages and enriched by incubation with the algal host. Until the host for the cyanophage(s) has been established one must use a spectrum of algal hosts.

In our laboratory we found that concentration by dialysis of even 3-4 liter samples of water required rather large volumes of PEG solutions (Desjardins, et al., 1978). We found that concentration of water samples could be obtained by either rotary evaporation or by high flow molecular filtration using the Millipore Pellicon Casette system. These two methods were found to be useful although tests indicated that 100% of infectious cyanophage concentrations were not recovered.

Although clarification of water samples by chloroform might be useful for some cyanophages, even rather low concentrations of this organic solvent can have deleterious effects on other cyanophages (Desjardins, et al., 1975).

PURIFICATION OF CYANOPHAGES. Once a cyanophage has been isolated and its host identified, the virus is purified from culture lysates so that its physical, chemical and biological properties can be characterized (Brown, 1972; Paden and Shilo, 1973; Safferman, 1973b; Sherman and Brown, 1978). It is, of course, necessary to have highly purified preparations of the cyanophages for the characterization of these properties.

Because there was loss of virus particle integrity when the AS-1 cyanophage was purified by techniques which utilized high shearing forces and compaction, such as differential and sharples centrifugation, we developed a method of purification which provided highly purified virus with high infectivity titers (Barkley and Desjardins, 1977). The method also overcame the osmotic effects that one encounters with PEG precipitation and $CsCl_2$ density gradient centrifugation (Desjardins, _et_ _al_., 1978). The method includes clarification of culture lysates with bentonite followed by low speed centrifugation. The supernatant is dialyzed against Tris-HCl buffer with Mg^{++}, concentrated by rotary evaporation and again dialyzed against the buffer. The supernatant of a second low speed centrifugation of the dialysate is subjected to sucrose density gradient centrifugation and then dialyzed to remove the sucrose. The final preparation is either given a low speed centrifugation or filtered through cellulose acetate membrane filters.

This method has proved very satisfactory for purifying the following cyanophages which are shown in Fig. 2: a) A-1[L] virus, which infects the filamentous alga _Anabaena_ _variabilis_; b) AS-1 virus, which infects the unicellular algae _Anacystis_ _nidulans_ and _Synechococcus_ _cedrorum_; and c) LPP-1 virus, which infects filamentous species in the genera _Lyngbya_, _Phormidium_ and _Plectonema_.

VIRUS PARTICLE MORPHOLOGY. As stated above the cyanophages are similar to bacteriophages in their morphological structures. The A-1[L] and AS-1 viruses have long tails with contractile sheaths (Fig. 2a and b). The LPP group of viruses have an icosahedral head with a short noncontractile tail (Fig. 2c) (Brown, 1972, Paden and Shilo, 1973, Safferman, 1973b, Sherman and Brown, 1978). The SM-1 virus has an icosahedral shape with no obvious tail (Safferman _et al_., 1969), and the S-1 virus has a hexagonal head with a long noncontractile tail (Sherman and Brown, 1978).

All the cyanophages characterized to date have been shown to contain linear, double stranded DNA (Padan and Shilo, 1973; Sherman and Brown, 1978).

ADSORPTION KINETICS AND GROWTH CURVES. The adsorption kinetics of various cyanophages to their hosts are essentially similar to those found for bacteriophages and their hosts although they may not always be first order reactions (Barkley, 1976; Mendzhul _et al_., 1974) The adsorption rate of the N-1 virus to its host _Nostoc muscorum_ could be increased by increasing the host cell density (Adolph and Haselkorn, 1972), but the rate of adsorption of AS-1 virus to _A_. _nidulans_ was not altered by increasing host cell concentration (Barkley, 1976). The adsorption of AS-1 cyanophage to one of its hosts, _S_. _cedrorum_, is similar to that of long-tailed bacteriophages to their hosts (Desjardins and Barkley, 1972) and is shown in Fig. 3a.

The one step growth curves of cyanophages are similar in shape to one step growth curves of bacteriophages (Adolph and Haselkorn, 1972; Barkley, 1976; Padan and Shilo, 1973; Sherman and Brown, 1978). This can be described as having a latent period followed by an exponential increase in extracellular virus which in turn is followed by a plateau when all infected cells have lysed. The length of the growth cycle can be altered by changing the conditions of culture. For example Barkley (1976) by utilizing aerated cultures of _A_. _nidulans_ inoculated with AS-1 virus cultures was able to reduce the

Figure 2. Examples of well characterized cyanophages: (a) the A-1 [L] virus which infects A. variabilis; (b) the AS-1 virus whose unicellular hosts are A. nidulans and S. cedrorum; and (c) the LPP-1 virus which infects species in the genera Lyngbya, Phormidium and Plectonema (Bars represent 250 nm.)

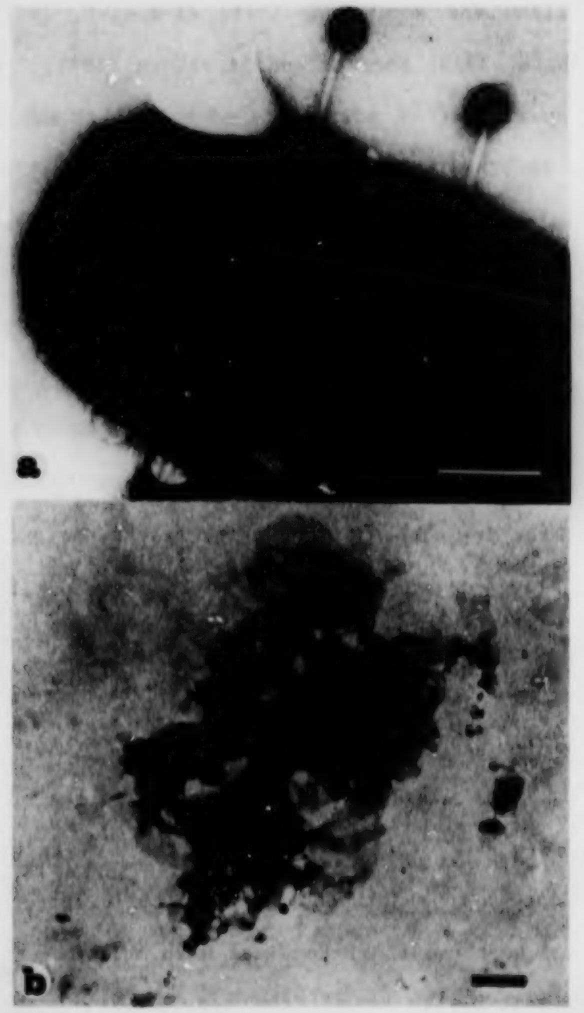

Figure 3. (a) AS-1 virus particles adsorbed to cell of S. cedrorum (Bar represents 250 nm); (b) Lysed single cell of A. nidulans infected with AS-1 cyanophage (Bar represents 500 nm.)

latent period by about one-half that found by Safferman *et al.* (1972) utilizing different culture methods.

One very interesting aspect of the replication of cyanophages in their host is the requirement that photosynthesis be not impaired (Adolph and Haselkorn, 1972; Allen and Hutchison, 1976; Al-Musavi, 1977; Padan *et al.*, 1970; Padan and Shilo, 1973; Sherman and Haselkorn, 1971). Cseke and Farkas (1979) have also shown that at low levels of Na^+ (11.7 mM) the total amount of AS-1 cyanophage adsorbed to *A. nidulans* was doubled in illuminated cultures as compared with cultures in the dark, and this was true over a wide range of multiplicities of infection.

According to Adolph and Haselkorn (1972) in their work with N-1 virus infections of *N. muscorum*, CO_2 fixation is not essential for virus replication; in fact they found a reduced photoassimilation of CO_2 between 4 and 5 hours after infection. They indicated that photosynthesis appeared to be necessary only for the production of adenosine triphosphate (ATP). Padan and Shilo (1973) have also pointed out that if an adequate supply of ATP is provided LPP cyanophages can replicate in the dark and under conditions which inhibit host growth (such as lack of any external carbon sources).

ASSAY OF LYTIC CYANOPHAGES. Lytic cyanophages are capable of producing plaques on lawns of their algal hosts. Plaques are areas on the algal lawns where host cell lysis has occurred starting with a single lysed cell and followed by virus spread to adjacent cells with their subsequent lysis. The mixture of virus and host cells are combined with melted agar and poured as a "soft" overlay on previously solidified agar layers. This technique is utilized to determine the number of infectious units (plaque forming units or pfu) in the original virus suspension. Lysis of a single cell of *A. nidulans* infected with AS-1 virus is illustrated in Fig. 3b.

Uniform lawns of unicellular algal species are obtained rather easily. Uniform lawns of filamentous species are not readily obtained unless the filments are broken into shorter trichomes. This can be done by controlled sonication of cell suspensions (Desjardins, et al., 1978). Sonication times and intensities must be determined for the species being studied and the sonication device available. Prolonged sonication can result in excessive cell degradation which precludes lawn formation.

An individual cyanophage strain grown in a particular host strain may vary in its ability to form plaques if assayed on a different host strain. This variation is based on the comparison with its plaque forming ability when assayed on the strain in which it was grown. This variation is often referred to as efficiency of plating. In their work with cyanophage N-1 and various strains of Anabaena, Currier and Wolk (1979) found that the efficiency of plaque formation could be increased by manipulating different characteristics of phage-host interaction. They demonstrated that growth of A. variabilis at 40°C for three generations resulted in a marked increase of efficiency of plating of the phage originally grown in another Anabaena strain (7120). They suggested that the original difference in plating efficiency in the two hosts may be partially due to the presence of a DNA restriction endonuclease in A. variabilis which is absent from Anabaena 7120.

One cannot help but wonder how important this variation in "efficiency of infection" may be in the interaction of cyanophages with their hosts in nature.

BIOLOGICAL CONTROL POTENTIAL OF CYANOPHAGES, POSSIBLE PROBLEMS

As stated in the introduction some research workers feel that the cyanophages have potential for serving as biological control agents for nuisance blue-green algae when introduced by man into natural water bodies. There are certain aspects of the interaction of the cyanophages with their hosts, and certain environmental and ecological factors, which might be possible problems from the standpoint of practical application of cyanophages for nuisance algal control. We might briefly consider some of these possible problems.

LYSOGENY. Up to this point we have discussed only lytic cyanophages. It is important that we consider temperate phages (i.e. those capable of entering into a lysogenic relationship with their hosts) and consider what role these temperate phages might play in the ecology of their hosts. A number of reports on the lysogeny of cyanophages have appeared (Cannon, 1975; Cannon, *et al*., 1971 and 1974; Khudyakov and Gromov, 1973; Padan, *et al*., 1972; Pahdy and Singh, 1978b; Rimon and Oppenheim, 1975; Sherman and Brown, 1978; Singh and Singh, 1972). Conclusive demonstration of lysogeny has been somewhat difficult with the cyanophages and their hosts because of problems in inducing the lytic stage by the usual methods (e.g. ultraviolet light or mitomycin C treatment). According to Sherman and Brown (1978) in some instances immunity studies were not performed and this casts doubt on whether lysogeny had occurred. However, the isolation of cyanophage strain LPP-2SP1 and a temperature-sensitive mutant of this strain provided unequivocal evidence that lysogeny does occur. The temperature-sensitive mutant lysogenized *Plectonema* in a stable manner at 26°C, but when the lysogenized cells were grown at 40°C, induction took place with the production of progeny phage. This finding permitted the initiation of studies on the biochemistry and physiology of lysogeny (Sherman and Brown, 1978).

The question arises as to whether the development of temperate mutants of cyanophages presents a problem for the biological control potential of cyanophages in natural bodies of waters. Since it is difficult to extrapolate the results of laboratory studies to field studies and since it is difficult to approach experimentally, one cannot readily discern whether it presents a problem or not.

Cannon (1975) has suggested that lysogeny might permit survival of both the virus and algal host at a low population density where environmental conditions were not ideal for either one. Presumably later, when conditions for both were more ideal, virus particles could be released by either spontaneous or chemical induction to control blooms of susceptible algal populations. This hypothesis could account for the non-blooming nature of *Plectonema boryanum*.

In any event with our present knowledge, one cannot readily determine whether or not lysogeny does present a problem for biological control in the field.

DEVELOPMENT OF RESISTANT HOST STRAINS. Growth of an algal host in continuous culture in the presence of the cyanophage provides a selection pressure on the host which results in the increased production of mutants which are resistant to the virus. Cowlishaw and Mrsa (1975) were able to demonstrate this with a cloned isolate of the filamentous blue-green alga, *Plectonema boryanum*, which was allowed to reach a steady state in a quasi-continuous culture in the presence of the LPP-1 cyanophage. After 3.5 months, during which time at least four distinct culture lysings occurred, the culture reached an algal concentration equal to the preinfection level. They found that cyanophage variants evolved during the process. They also found that host cell variants that evolved were resistant to both the original virus and the evolved virus. In addition they found no evidence of lysogeny among the algal cells. The evolved virus was serologically related to the original virus and still grew on the parental alga strain but with an altered plaque morphology. They did find, however, that a low-grade chronic viral infection persisted in the culture.

Cannon *et al*. (1976) made a somewhat similar study utilising a culture apparatus which had been converted into a chemostat. In addition to the lytic LPP-1 cyanophage, they used two temperate cyanophages in the LPP group, namely LPP-1D and LPP-2. Resistant algae eventually populated the chemostat with all three cyanophages, and lysogeny did not appear to be established. They stated that the interaction between the resistant *Plectonema* and the three LPP cyanophages resulted in rapid loss of the viruses from the chemostat apparatus. When lysogenic *P*. *boryanum* was tested, a low titer of virus was present throughout the incubation period which indicated that spontaneous induction was occurring.

Jenifer (1977) studied the development of strains of *Anacystis* *nidulans* which were resistant to the AS-1 cyanophage, although he obtained the resistant host strain in a culture which did not involve provision for a steady state culture to develop. He found that very little AS-1 virus was adsorbed to the resistant strain of *A*. *nidulans* while the sensitive original alga strain adsorbed approximately 90% of the virus.

The results of the above studies suggest that the development of host strains that are resistant to their cyanophages might be a limiting factor and a problem in the use of cyanophages as biological control agents for nuisance blue-green algae. The development of resistant strains may indeed be a problem, but there are certain aspects of the problem which were not considered in these laboratory studies, but which might play a role under natural conditions. It does not seem reasonable that results of laboratory studies with axenic cultures can be completely extrapolated from the laboratory conditions to conditions existing in a large body of natural water (Desjardins, *et* al., 1978; Safferman, personal communication). This conclusion is based on the following: 1) There is no reason to believe that the evolved virus-resistant strain could survive in nature against other factors that might adversely affect the alga any more readily than the virus-susceptible strain, 2) the extrapolation of results of laboratory studies to the natural habitat overlooks the succession of species which occurs in nature when one species declines (Fogg, 1965; Lin, 1972), and 3) there is always the possibility that under natural conditions the evolution of the virus might provide a viral strain which could infect the algal strain which developed resistance to the original virus.

Also a number of observations made in field studies suggest that resistant strains may not play a dominant role. Safferman and Morris (1967) and Padan and Shilo (1969) in studies on the distribution of cyanophages observed that susceptible algal genera were never dominant in habitats where the cyanophages were found. They suggested that possibly a population equilibrium between them was established. Cannon (1975) has also stated that although one might expect development of resistant algal populations after large virus infections, this has not been confirmed during exhaustive field studies.

Another observation in our laboratory a few years ago is also of some interest in this regard (Desjardins and Barkley, unpublished). During studies of the AS-1 cyanophage and one of its hosts, A. nidulans, we obtained a culture of the alga which appeared to be resistant to AS-1 virus. We wondered at the time if possibly a lysogenic relationship had been established between the virus and its host. Our attempts to demonstrate lysogeny by induction of the lytic cycle with both UV irradiation and mitomycin C treatment were unsuccessful. We therefore assumed that a resistant algal strain had developed. Because of other research interests at the moment, we set the culture aside temporarily but kept it under culture with regular transfers. We did not clone the resistant culture but simply maintained it over a period of several months. Sometime later when we decided to study the culture further from the standpoint of phage adsorption to cells, we found that the culture was again susceptible to the AS-1 virus. Apparently susceptible cells had once again become the dominant cell type in uncloned culture. Perhaps in nature the removal of the selection pressure, by a temporary absence of the virus, might also result in the reemergence of dominance of a susceptible cell population.

In any event, it would appear that until results of field studies prove otherwise, one cannot say unequivocally that the development of host resistant strains will preclude the use of cyanophages as biological control agents.

EFFECTS OF ENVIRONMENTAL FACTORS. Although it is fairly easy to study the effects of such environmental factors as light, temperature, pH and ionic environment under controlled laboratory conditions, the effects of these factors under natural conditions cannot be so readily ascertained because of possible interaction of the factors, physical size, etc. Nevertheless if variation of a particular factor adversely affects the infection of and multiplication in the host by a cyanophage in the laboratory, it does not seem unreasonable to assume that a similar effect might occur in a natural water body. For example, if localised conditions in a water body impair photosynthesis in the algal host (which was discussed earlier), one might expect that cyanophage adsorption and multiplication might be adversely affected.

Considering light intensity as a factor, in dense algal blooms there may be levels where this factor might be important. It has been suggested that gas vacuoles in blue-green algae might, by affecting the buoyancy of the cells, permit the cells to move to levels of light intensity ideal for photosynthesis (Walsby, 1972). If this is true, perhaps the adverse effects of low light intensities on cyanophage growth might be partly overcome.

Intensive studies of the effects of temperature on cyanophage infections have apparently not been made. Certainly temperature extremes that greatly affect the host might be expected to have some sort of effect on virus infection. It has been shown that temperature does affect the adsorption and multiplication of certain aquatic bacteriophages (Seeley and Primrose, 1980), and it is not inconceivable that certain cyanophage strains might be similarly affected by pronounced temperature variations. Certain strains of LPP-1 cyanophage have a greater capacity to form plaques at 26°C than at 35°C (Safferman, 1973b). It is not likely that large bodies of water in temperate zones would have extremely high temperatures, but temperature-sensitive strains might be less efficient in their infection capabilities at the higher temperatures reached in shallow water bodies during the warmest part of the season.

Low temperatures above freezing (ca 4°C) do not adversely affect the LPP-1, SM-1 and AS-1 cyanophages (Safferman, 1973; Safferman, et al., 1969; Safferman et al., 1972), but freezing does destroy the integrity of the AS-1 virus particle (Desjardins, et al., 1975). Although a large body of water would probably not completely freeze, freezing of the upper levels might reduce the titer of infectious virus in the water body.

The pH of a water body is another environmental factor which should be considered. Safferman and Morris (1964) found the LPP-1 virus to be stable from pH 7 to 11 and that substantial growth of its host P. boryanum occurred within this pH range. Mendzhul et al. (1974) found, however, that although adsorption of LPP-1 to its host occurred over the range of pH 7 to 11, it was somewhat reduced at pH values above 8. Safferman *et al*. (1969) found the SM-1 cyanophage to be stable over the same pH range, but found some loss of infectivity at the extremes of this range. The AS-1 virus was found to be stable over an even greater range (i.e., between pH 4 and 10) but a 75% reduction in infectious virus titer occurs at pH 11. Padhy and Singh (1978a) found the rate of adsorption of N-1 virus to *Nostoc muscorum* had an optimal pH range of 7.6 to 8.1 and a reduced rate at pH values of 9 and 10.

It appears that pH ranges on the alkaline side of neutrality (except very high pH values) would not be a critical factor under natural conditions, especially since such pH values are ideal for the host also.

One might consider the ionic environment as a factor in the control of their hosts by cyanophages, although there is not much experimental data upon which to base an assessment. It has been shown that Mg^{++} ion is necessary for the stability of LPP-1 virus (Safferman, personal communication) and for its adsorption to its host (Mendzhul, *et al*., 1974), but the required concentrations are low, and therefore should not be a limiting factor. One must wonder, however, what effect extremely high salt concentrations might have on cyanophage-host interaction and on cyanophage stability. It is conceivable that high salt concentrations might affect adsorption of virus particles to organic debris and also might have an osmotic effect on the virus particle itself. Such effects have yet to be investigated.

Because the LPP-1 virus is more resistant to chlorination than coliform bacteria, it has been suggested that it be used to predict the presence of animal viruses in sewage effluents, and that it could be used for such prediction in place of the coliform test (Smedberg and Cannon, 1976). The resistance of LPP-1 and other cyanophages to various concentrations of other anions should be investigated to see what effect they might have on the survival of these viruses.

CELL SHEATH AND CELLULAR DEBRIS. According to Sanger and Dugan (1972) the production of extracellular polysaccharides by A. nidulans is dependent upon the age of culture, the growth temperature and the form of available nitrogen. They also state that the production of large amounts of extracellular polysaccharide can contribute to the eutrophication of water by organic enrichment. One cannot but wonder if the mere physical presence of cellular sheath material might not interfere with the adsorption of cyanophages to their hosts. The rather extensive sheath of P. boryanum is shown in Fig. 4b. The filaments of P. boryanum shown in Fig. 4 are from the same culture. If age of cells plays a role in sheath production of this species also, the presence of a sheath on some filaments and its absence on others (Fig. 4a) might be explained on an age basis since the culture was not a synchronous culture.

Schnayer and Jenifer (1974) and Samimi and Drews (1978) have isolated the receptor site of AS-1 virus from its host A. nidulans and have shown it to be a lipopolysaccharide. They have also shown that the isolated receptor material can inactivate the virus. The possibility that receptor material may be present and accessible on the cellular debris upon virus induced lysis of host cells should be investigated. If it does remain intact and active, it is conceivable that the infectious titer of cyanophages in natural water could be reduced by the lysis of large numbers of host cells.

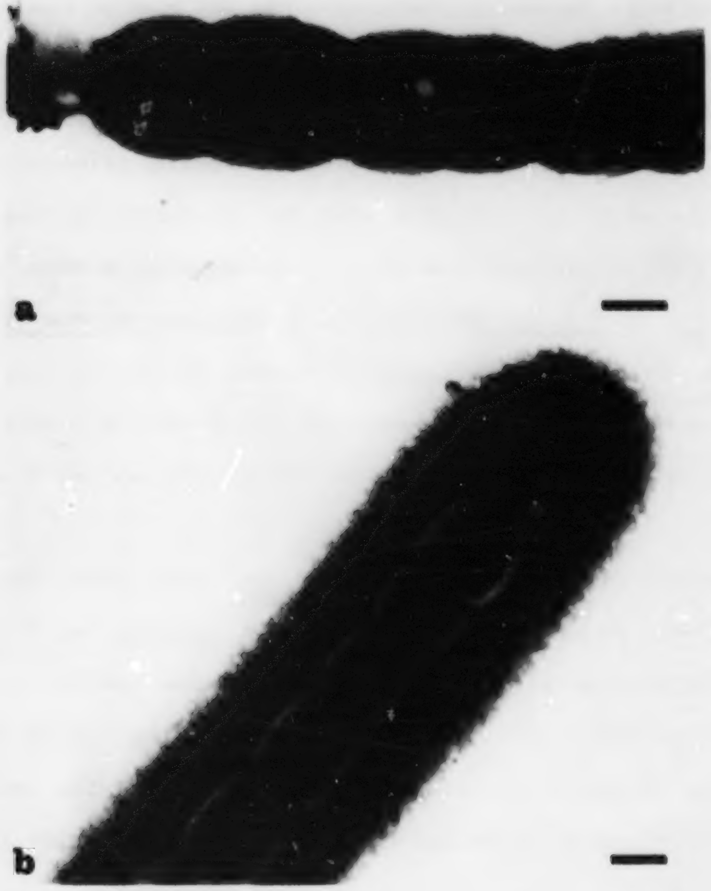

Figure 4. Electron micrographs of negatively stained preparations of P. boryanum from aerated cultures: (a) Tip of filament without mucilaginous sheath; (b) Tip of filament with mucilaginous sheath (Bars represent 1 μm.)

ATTEMPTS AT VIRAL CONTROL OF BLUE-GREEN ALGAE

As stated earlier, subsequent to the first report by Safferman and Morris (1963) of the isolation of the LPP-1 cyanophage, several viruses and virus strains which infect unicellular or filamentous blue-green algae have been reported. The emphasis of research has been on the purification of these viruses and the characterization of their physical, chemical and biological properties. Although this emphasis of research efforts is understandable because of the novelty of the virus group, it is still somewhat puzzling as to why greater efforts have not been made to demonstrate their control potential. Partial explanation of this lack of effort was due to the realization that certain basic knowledge of the viruses and their properties is essential for the selection of approaches to testing the actual control potential.

Jackson and Sladecek (1970) made one of the first attempts to actually control blue-green algae in a natural habitat. They attempted to establish _P. boryanum_ in 5000-gallon tanks at a sewage treatment plant in order to test the LPP-1 virus against this host. Over 40 attempts were made to establish the host in the tanks and all were unsuccessful. The LPP-1 virus was already naturally present and was controlling the algal host and preventing its establishment.

It has been reported that Russian workers have controlled blue-green algal scums as a result of spraying cyanophages on infested waters (cited in Peelen, 1969). The cyanophages utilized and their hosts were not described.

In our laboratory we have controlled _A. nidulans_ with AS-1 cyanophage and _P. boryanum_ with LPP-1 cyanophage in 90-liter plastic tank cultures in temperature baths in the greenhouse (Fig. 5) (Desjardins, _et al._, 1978). The LPP-1 virus has become so well established in the facility that we can no longer grow P. boryanum, even though we steam-sterilize the plastic tanks which actually contain the algal culture.

In more recent work we have attempted to control P. boryanum in 8000-liter outdoor ponds (Desjardins and Olson, unpublished). In order to establish the alga, we had to enrich the pond with nutrients. This was done by adding modified Hughes medium to 0.1 the strength used in laboratory cultures. A good bloom was established and P. boryanum was controlled based on microscopic observations of plated cultures of samples taken at various times after introduction of the cyanophage. However, other blue-green and green algal species replaced the P. boryanum. Because of this the pond water did not clear, but simply had a bloom involving other species. This serves to point out the fact that a broad spectrum of cyanophages must be available for controlling succeeding species as well as initial bloom species.

DISCUSSION, RESEARCH NEEDS AND PRIORITIES

In this paper I have attempted to briefly summarize the information on cyanophages that is in any way related to their potential as biological control agents. Also I have attempted to describe possible problems which should be considered both with respect to the assessment of algal control potential and to further research needs and priorities. It is my opinion that cyanophages do appear to have biological control potential but that certain areas of research should be intensively pursued.

As suggested in the discussions of this workshop on Algal Management and Control, an integrated approach utilizing all available methods of biological control might prove to be the most fruitful for the desired management and control of nuisance species. Methods would include the ecosystem manipulation (biomanipulation) suggested by Shapiro, et al. (1975), the use of bacterial agents as recommended by Burnham (1975) and Burnham et al. (1976), and the use of single or multiple cyanophages. In regard to microbial agents, the

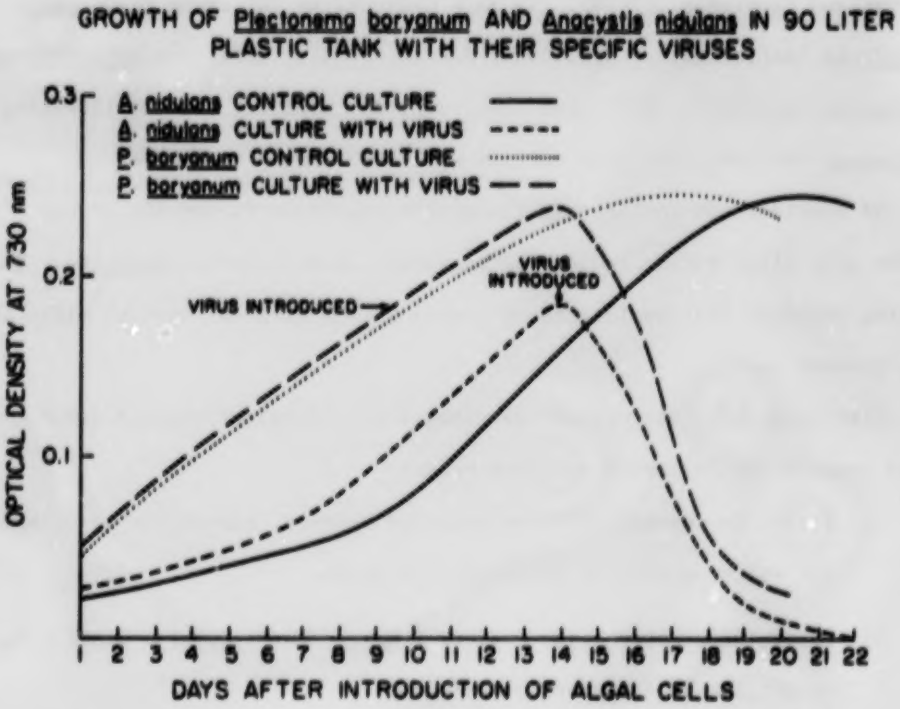

Figure 5. Graphic illustration of the control of *A. nidulans* and *P. boryanum* by their cyanophages (AS-1 and LPP-1 respectively) in 90-liter tank cultures

Myxococcus species described by Burnham at this workshop would appear to be especially promising for an integrated approach.

Some discussion of toxic blue-green algal species should be included in considering biological control. The most frequently found toxic blue-green algae are Microcystis aeruginosa, Anabaena flos-aquae and Aphanizomenon flos-aquae (Hughes, et al., 1958; Collins, 1978; Gorham and Carmichael, 1979), but toxic isolates have also been found in Lyngbya, Schizothrix, and Synechococcus (Gorham and Carmichael, 1979). To date cyanophages infecting Microcystis aeruginosa (Safferman, et al., 1969; Martin, et al., 1978) and Aphanizomenon flos-aquae (Granhall, 1972) have been reported; however, the one infecting A. flos-aquae has been lost from culture and is no longer available.

Of considerable interest is the recent report by Porter and Orcutt (1980) that algal toxins reduce the survival capabilities of Daphnia. This finding suggests that an integrated approach to biological control might indeed be a prudent one.

With respect to the use of cyanophages as biological control agents, I would suggest the following research needs:

1) Search for cyanophages for nuisance species, especially toxic species, for which no viruses are presently known.

2) Determine whether virus-resistant host strains develop under natural conditions in large bodies of water.

3) More critically determine the role of lysogeny in the ecology of cyanophage-host interactions and how it might affect control.

4) Accurately determine the effect of environmental factors on the infection and survival capabilities of cyanophages.

5) Establish outdoor research facilities which would permit standardization of conditions, as far as possible, between control and cyanophage-treated waters.

6) Initiate tests utilizing presently available cyanophages in natural water bodies where their hosts have been a continuing nuisance.

7) Attempt to elucidate how toxic algal species arise-- do plasmids or viruses possibly play a role?

Support for research in these areas is necessary if any true progress is to be made in the evaluation of the biological control potential of cyanophages against their hosts in natural waters.

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REFERENCES

Adolph, K. W. and R. Haselkorn. 1972. Photosynthesis and the Development of Blue-Green Algal Virus N-1. Virology 47: 370-374.

Allen, M. M. and F. Hutchison. 1976. Effect of Some Environmental Factors on Cyanophage AS-1 Development in Anacystis nidulans. Arch. Microbiol. 110: 55-60.

Al-Musavi, R. A. 1977. Effect of photosynthesis and respiration on growth of cyanophages of Anabaena variabilis. Microbiologiya 46: 725-729.

Barkley, M. B. 1976. Ultrastructure of the blue-green alga Anacystis nidulans infected with the AS-1 virus. Ph.D. Thesis, University of California, Riverside.

Barkley, M. B. and P. R. Desjardins. 1977. Simple, Effective Method for Purifying the AS-1 Cyanophage. Appl. and Environmental Microbiol. 33: 971-974.

Brown, R. M., Jr. 1972. Algal viruses. Adv . Virus Res. 17: 243-277.

Burnham, J. C. 1975. Bacterial Control of Aquatic Algae, p. 120-125. Proc. Symp. Water Quality Management Through Biological Control, Rpt. No. ENV-07-75-1, Dept. Environ. Eng. Sci., Univ. of Florida.

Burnham, J. C., T. Stetak and G. Locher. 1976. Extracellular lysis of the Blue-green Alga Phormidium luridum by Bdellovibrio bacteriovorus. Jour. Phycol. 12: 306-313.

Cannon, R. 1975. Field and Ecological Studies on Blue-Green Algal Viruses, p. 112-117. Proc. Symp. Water Quality Management Through Biological Control. Report No. 07-75-1, Dept. Environ. Eng. Sci., University of Florida.

Cannon, R. E., M. S. Shane, and V. N. Bush. 1971. Lysogeny of a Blue-Green Alga, Plectonema boryanum. Virology 45: 149-153.

Cannon, R. E., M. S. Shane, and E. De Michele. 1974. Ecology of blue-green algal viruses. Jour. Environ. Eng. Div. ASCE 100: 1205-1211.

Cannon, R. E., M. S. Shane and J. M. Whitaker, 1976. Interaction of *Plectonema boryanum* (Cyanophyceae) and the LPP-cyanophages in continuous culture. Jour. Phycol. 12: 418-421.

Collins, M. 1978. Algal Toxins. Microbiol. Rev. 42: 725-746.

Cowlishaw, J., and M. Mrsa. 1975. Co-Evolution of a Virus-Alga System. Appl. Microbiol. 29: 234-239.

Cseke, CS. and G. L. Farkas. 1979. Effect of Light on the Attachment of Cyanophage AS-1 to Anacystis nidulans. J. Bact. 137: 667-669.

Currier, T. C., and C. P. Wolk. 1979. Characteristics of *Anabaena variabilis* Influencing Plaque Formation by Cyanophage N-1. Jour. Bact. 139: 88-92.

Daft, M. J., J. Begg and W. D. P. Stewart. 1970. A Virus of Blue-green Algae from fresh-water habitats in Scotland. New Phytol. 69: 1029-1038.

Desjardins, P. R. and M. B. Barkley. 1972. AS-1 virus adsorption to cells and spheroplasts of *Synechococcus cedrorum*, p. 332-333. *In* 30th Ann. Proc. Electron Microscope Soc. Amer.

Desjardins, P. R., S. A. Swiecki, M. B. Barkley and R. J. Drake. 1975. Effects of certain chemical treatments and freezing on the ultrastructure of the AS-1 phycovirus particle. Abstr. #C469. 3rd Intern. Congress for Virology, Madrid, Spain.

Desjardins, P. R., M. B. Barkley, S. A. Swiecki and S. N. West. 1978. Viral Control of Nuisance Blue-Green Algae. Contribution No. 169. California Water Resources Center., University of California.

Fogg, G. E. 1965. Algal Cultures and Phytoplankton Ecology. Univ. of Wisconsin Press.

Fogg, G. E. 1969. The Leeuwenhoek Lecture, 1968 - The Physiology of an Algal Nuisance. Proc. Roy. Soc. B. 173: 176-189.

Gorham, P. R. and W. W. Carmichael. 1979. Phycotoxins from blue-green algae. Pure and Appl. Chem. 52: 165-174.

Granhall, U. 1972. *Aphanizomenon flos-aquae*: Infection by Cyanophages. Physiol. Plant. 26: 332-337.

Hughes, E. O., P. R., P. R. Gorham and A. Zehnder. 1958. Toxicity of a Unialgal Culture of *Microcystis aeruginosa*. Can. J. Microbiol. 4: 225-236.

Jackson, D. and V. Sladecek. 1970. Algal viruses—eutrophication control potential. Yale Scientific Magazine 44: 16-21.

Jenifer, F. G. 1977. Studies on the natural relationships of cyanophages and their hosts and the nature of resistance. Completion Report, Water Resources Research Inst., New Brunswick, N. J.

Jenifer, F. G., N. J. Schnayer, M.-L. Chen and L. Carnegie. 1974. The occurrence, distribution, and seasonal incidence of cyanophages and their specific hosts in the same natural water system. Proc. Amer. Phytopath. Soc. 1: 137.

Krauss, R. W. 1961. Fundamental characteristics of algal physiology. p. 40-47. *In* Algae and Metropolitan Wastes. U.S. Dept. of Health, Education and Welfare. SEC TR W 61-3.

Khudyakov, I. Ya., and M. V. Gromov. 1973. The temperate cyanophage A-4 [L] of the blue-green alga *Anabaena variabilis*. Mikrobiologiya 42: 904-907.

Kozyakov, S. Ya. 1977. Cyanophages of series A(L), specific for blue-green algae *Anabaena variabilis*. p. 151-171. In B. V. Gromov, (Ed). Experimental Algology. Biological Scientific Res. Inst. Leningrad State University.

Lin, C. K. 1972. Phytoplankton succession in a eutrophic lake with special reference to blue-green algal blooms. Hydrobiologia 39: 321-334.

Martin, E. L., J. E. Leach and K. J. Kuo. 1978. Biological regulation of bloom-causing blue-green algae, p. 62-67. *In* Microbial Ecology, Springer-Verlag.

Mendzhul, M. I., S. P. Bobrovnik and T. G. Lysenko. 1974. Study of cyanophage LPP-1 adsorption on cells of cyanophyceae (*Plectonema boryanum*). Voprosy Virusologii 1: 31-36.

Padan, E., and M. Shilo. 1969. Distribution of cyanophages in natural habitats. Verh. Internat. Verein. Limnol. 17: 747-751.

Padan, E., D. Ginzberg and M. Shilo. 1970. The reproductive cycle of cyanophage LPP-1-G in *Plectonema boryanum* and its dependence on photosynthetic and respiratory systems. Virology 40: 514-521.

Padan, E., M. Shilo and A. B. Oppenheim. 1972. Lysogeny of the blue-green alga *Plectonema boryanum* by LPP2-SP1 cyanophage. Virology 47: 525-526.

Padan, E. and M. Shilo. 1973. Cyanophages -- Viruses attacking blue-green algae. Bact. Rev. 37: 343-370.

Pahdy, R. N. and P. K. Singh. 1978a. Effects of host aging, ions, and pH on the adsorption of the cyanovirus N-1 to *Nostoc muscorum*. Arch. Microbiol. 116: 289-292.

Pahdy, R. N. and P. K. Singh. 1978b. Lysogeny in the blue-green alga *Nostoc muscorum*. Arch. Microbiol. 117: 265-268.

Palmer, C. M. 1977. Algae and Water Pollution EPA-600/9-77-036. Environ. Protection Agency, Cinncinati, OH.

Peelen, R. 1969. Possibilities to prevent blue-green algal growth in the Delta region of the Netherlands. Verh. Internat. Verein. Limnol. 17: 763-766.

Porter, K. G. and J. D. Orcutt, Jr. 1980. Nutritional adequacy, manageability, and toxicity as factors that determine the food quality of green and blue-green algae for Daphnia, p. 1-35. In A.S.L.O. Special Symp. III: The Evolution and Ecology of Zooplankton Communities.

Rimon, A. and A. B. Oppenheim. 1975. Heat induction of the blue-green alga Plectonema boryanum lysogenic for the cyanophage SPlctsl. Virology 64: 454-463.

Safferman, R. S. 1968. Virus diseases in blue-green algae, p. 429-439. In D. F. Jackson [ed.], Algae, Man and the Environment. Syracuse Univ. Press.

Safferman, R. S. 1973a. Special methods - virus detection in Cyanophyceae. p. 145-158. In J. R. Stein (Ed.) Handbook of Phycological Methods - Culture methods and growth measurements. Cambridge University Press.

Safferman, R. S. 1973b. Phycoviruses, p. 214-237. In N. G. Carr and B. A. Whitton [ed.], The Biology of Blue-green Algae. Blackwell Sci. Pub.

Safferman, R. S. and M. E. Morris. 1963. Algal virus: isolation. Science 140: 679-680.

Safferman, R. S. and M. E. Morris. 1964. Control of algae with viruses. Jour. Amer. Water Wks. Assoc. 56: 1217-1224.

Safferman, R. S. and M. E. Morris. 1967. Observations on the occurrence, distribution, and seasonal incidence of blue-green algal viruses. Appl. Microbiol. 15: 1219-1222.

Safferman, R. S., I. R. Schneider, R. L. Steare, M. E. Morris and T. O. Diener. 1969. Phycovirus SM-1: A virus infecting unicellular blue-green algae. Virology 37: 386-395.

Safferman, R. S., T. O. Diener, P. R. Desjardins and M. E. Morris. 1972. Isolation and Characterization of AS-1, a Phycovirus infecting the blue-green algae, *Anacystis nidulans* and *Synechococcus cedrorum*. Virology 47: 105-113.

Safferman, R. S. and M. E. Rohr. 1979. The Practical Directory to Phycovirus Literature. EPA-600/9-79-013. Environ. Protection Agency. Cincinnati, OH.

Samimi, B. and G. Drews. 1978. Adsorption of Cyanophage AS-1 to Unicellular cyanobacteria and isolation of receptor material from *Anacystis nidulans*. J. Virology 25: 164-174.

Sangar, V. K. and P. R. Dugan. 1972. Polysaccharide produced by *Anacystis nidulans*: its ecological implications. Appl. Microbiol. 24: 732-734.

Schnayer, N. and F. G. Jenifer. 1974. Inactivation of blue-green alga virus, AS-1, by isolated host lipopolysaccharide. Proc. Amer. Phytopath. Soc. 1: 144.

Seeley, N. D. and S. B. Primrose. 1980. The effect of temperature on the ecology of aquatic bacteriophages. J. Gen. Virol. 46: 87-95.

Shane, M. S. 1971. Distribution of blue-green algal viruses in various types of natural waters. Water Res. 5: 711-716.

Shane, M. S., R. E. Cannon and E. DeMichele. 1972. Pollution effects on phycovirus and host algae ecology. J. Water Pollution Control Federation 44: 2294-2302.

Shapiro, J., V. Lamarra and M. Lynch. 1975. Biomanipulation: An ecosystem approach to lake restoration, p. 85-96. Proc. Symp. Water Quality Management Through Biological Control. Rpt. No. ENV-07-75-1 Dept. Environ. Eng. Sci., University of Florida.

Sherman, L. A. and R. Haselkorn. 1971. Growth of the blue-green algal virus LPP-1 under conditions which impair phytosynthesis. Virology 45: 739-746.

Sherman, L. A. and R. M. Brown, Jr. 1978. Cyanophages and Viruses of Eukaryotic Algae. In H. Fraenkel-Conrat and R. R. Wagner [eds.] Comprehensive Virology 12: 145-234.

Shilo, M. 1969. New approaches to the control of harmful brackish and fresh water algae of economic importance. Biotech. and Bioeng. Symp. 1: 177-184.

Shilo, M. 1971. Biological agents which cause lysis of blue-green algae. Mitt. Internat. Verein. Limnol. 19: 206-213.

Shilo, M. 1972. The ecology of cyanophages. Bamidgeh 24: 76-82.

Singh, R. N. and P. K. Singh. 1972. Transduction and lysogeny in blue-green algae, p. 258-261. In T. V. Desikachary [ed.] Taxonomy and Biology of Blue-Green Algae. Univ. of Madras. Press.

Smedberg, C. T., and R. E. Cannon. 1976. Cyanophage analysis as a biological pollution indicator--bacterial and viral. Water Poll. Control. Fed. Jour. 48: 2416-2426.

Walsby, A. E. 1972. Structure and Function of Gas Vacuoles. Bact. Rev. 36: 1-32.

THE UTILIZATION OF BACTERIA IN MANAGING CYANOBACTERIAL POPULATIONS: A REVIEW AND UPDATE

Jeffrey C. Burnham
Department of Microbiology
Medical College of Ohio
C. S. 10008
Toledo, Ohio 43699

INTRODUCTION

This review will examine a series of papers which have utilized a blend of bacterial physiology and cytology to examine and solve a problem in applied ecology, i.e., how to utilize bacterial populations to control the growth of different cyanobacterial species in natural aquatic habitats. As the earlier papers presented at this conference have amply demonstrated, cyanobacterial problems dominate in many of the lakes and reservoirs in the United States. As nitrates and phosphates accumulate from soil runoff, the waters become eutrophic and the cyanobacterial populations proliferate rapidly to undesirable levels, causing taste and odor problems, poor aesthetics and occasionally toxic gastroenteritis if ingested by man or animals. Most significantly, as these cyanobacterial populations die and decay, the dissolved oxygen in the water is depleted, leading to a total disruption of the desired aquatic ecosystem balance. The rationale of using bacterial biological control agents is to prevent the accumulation of cyanobacteria to noxious levels by applying an interspecies antagonism, i.e., by either inhibiting the growth of or lysing the cells of the cyanobacterial pests. This is amplified by a quotation from Huffaker and Messenger's (1976) book entitled Biological Control: "If we are to reverse the trend toward an ever intensified overloading of the environment with polluting and highly toxic pesticides, we must show that biological control, combined with restricted usage of selective chemicals . . . and other integrative measures can, in fact, solve many of our pest problems without resort to disturbing and polluting chemicals."

THE NATURE OF THE PREY

If one is to devise a strategy to effectively antagonize a group of organisms, it is important to consider the basic properties of these organisms, as well as to examine specific characteristics of the organisms that would provide benefit to a predator. The cyanobacteria occupy a unique phylogenic and evolutionary niche in nature. Until recently (Buchanan and Gibbons, 1974) these organisms were considered algae and allied closer to the plant kingdom. Their properties are well documented (Fogg _et al_., 1973) and their procaryotic structure is well established (Lang, 1968), bringing them closer to the bacteria in structure and function. This is important to the philosophy of attacking them in aquatic ecosystems. As outlined in Table 1, there are many properties of these cyanobacteria that directly affect the feasibility of bacteria being successful cyanobacterial predators. Their autotrophic metabolism allows these cyanobacteria to convert inorganic nutrients to organic cell constituents. The fact that many cyanobacterial species are abundant in eutrophic waters makes them one of the primary sources of heterotrophic nutrient present in fresh water ecosystems. Unfortunately, for most aquatic bacterial species, this nutrient source is simply unavailable. A successful strategy of an effective predator would be to utilize this common nutrient source to its advantage. The cyanobacterial properties of aerobic growth in surface waters while secreting oxygen and carbohydrate provide both a natural attraction for bacteria and a suitable environment for an oxygen-utilising predator to operate. Their common filamentous property, although providing problems to the investigator studying cellular kinetics, provides a microbial parasite a mechanism with which to engangle the prey. The flocculent clumping that results provides an enormous increase in surface area for continued collection of suspended cyanobacteria. The procaryotic characteristics of a peptidoglycan cell wall layer (Lang, 1968) offers potential cyanobacterial vulnerability to bacterial cell wall lytic exoenzymes and antibiotics. This character will be extensively developed later in this presentation. Finally, the observation that given considerable stress (Burnham, et al., 1976; 1977) cyanobacteria are capable of lysing under the primary influence of their own enzymes— a property which only enhances the production of available heterotrophic nutrient upon cyanobacterial dissolution--will be discussed.

CYANOBACTERIAL/BACTERIAL RELATIONSHIPS

Although the interactions between bacteria and cyanobacteria involve symbiotic, commensal, neutral or antagonistic relationships, there have been serious efforts to examine the requirements of either partner for interaction and the resulting nutrient and gaseous exchange between the species. The dominant relationship appears one of symbiotism (Lange, 1970) and with the carbonaceous and nitrogenous excretions of the cyanobacteria (Fogg, 1952) being assimilated by the bacteria, and the bacterial-produced carbon dioxide resulting in accelerated cyanobacterial photosynthesis (Lange, 1971). This relationship was elegantly illustrated in an electron microscopic study by Paerl (1976) of bacteria colonizing the nitrogen-fixing heterocysts of Anabaena and Aphanizomenon species. Because atmospheric CO_2 probably becomes limiting during intensive photosynthesis, the CO_2 producing role of bacteria may be certainly beneficial to the rapid growth of the cyanobacteria. This relationship was shown by Lange (1971) to be enhanced with CO_2 production by the symbiotic bacteria was increased by adding various organic substrates and could be mimicked by supplying additional CO_2 to the cyanobacterial culture.

TABLE 1

Characteristics of Cyanobacteria Influencing Their Role as Microbial Prey

abundance in eutrophic waters

autotrophic metabolism

aerobic

growth in surface waters

oxygen producers

secrete carbohydrates

filamentous

peptidoglycan cell wall component

autolytic mechanism

heterotrophic nutrient release upon lysis

This nutrient exchange between symbiotic or commensal bacteria and cyanobacteria only enhances the concept that cyanobacterial organic compounds could serve as a major nutrient for a bacterial prey species.

Although symbiotism is common, non-specific antagonism also occurs. Fitzgerald (1969) showed that bacteria-containing sewage effluents would support the growth of the green alga Chlorella but would not allow the growth of the cyanobacterium Microcystis aeruginosa. When the bacteria were removed by autoclaving or filtration, the M. aeruginosa were able to thrive. Gunnison and Alexander (1975) in a study examining why certain algae could be naturally degraded by microbial enzymes showed that the peptidoglycan component of cyanobacteria (blue-green algae) provides the weak link in these organisms' armor against microbial lysis. Fallon and Brock (1979) enlarged on this concept of microbial lysis of algae by examining the decomposition and mineralization of cyanobacteria in a lake in Wisconsin. They concluded that the bacteria responsible for cyanobacterial degradation depended upon the products of that degradation for all of their nutritional needs. Although these authors report a lytic bacterial level of 10^3 cells per ml of tested lake water, they did not identify the bacterial decomposer species. The remainder of this review will examine specific antagonistic relationships between bacteria and cyanobacteria.

BACTERIAL ANTAGONISM FOR CYANOBACTERIA

Table 2 provides a list of the bacterial systems that are capable of causing the lysis of cyanobacterial populations. I should point out that other microorganisms, specifically various protozoa, fungi and cyanophage, are also capable of lysing cyanobacteria but these will not be considered in this presentation. I have discussed many of the lytic bacteria in a previous review (Burnham, 1975), so I will highlight only a few in this presentation. Bacterial lytic secretions without direct cell-to-cell interaction explain the mechanism of lysis for most of the lytic genera listed in Table 2. Actinomycetes, Streptomyces, Bacillus, Pseudomonas, Cellvibrio and Bdellovibrio cell-free culture supernatant preparations have been reported to contain cyanobacterial lytic substances, either exoenzymes or antibiotics. Because the cyanobacterial antagonism that results from these interactions depends upon the concentration of these lytic substances in the environment, I do not believe they offer potential as practical control agents. My own earlier efforts utilizing Bdellovibrio bacteriovorus (Burnham, 1975; Burnham et al, 1976a; Burnham et al., 1976b;Burnham and Sun, 1977; Burnham, 1977) evinced an interesting inhibitor of cyanobacterial photosynthesis of low molecular weight that triggered an autolytic dissolution of the photosynthetic lamellae. Such a photosynthetic toxin was appealing as a control agent but my laboratory has not been successful in stimulating the production of this inhibitor without large additions of protein to the Bdellovibrio culture. Until we can demonstrate the production of this inhibition without direct substrate addition we do not believe the Bdellovibrio system can be of significance in environmental cyanobacterial control.

The lysis of cyanobacteria by the myxobacteria in my opinion offers the best potential at the present time for a successful biological control agent for unwanted cyanobacteria. Ever since Shilo (1967) showed that myxobacteria were capable of lysing various species of cyanobacteria, evidence has been accumulating which only heightens this potential.

Shilo's discovery simply expanded upon the knowledge that myxobacteria are one of the most potent bacteriolytic microbial organisms known. Early data (Beebe, 1941) indicates that these organisms were readily able to lyse living host bacterial populations. This lytic characteristic is due to its ecological niche as a soil bacterium and, in addition, to

TABLE 2

Bacterial Lytic Systems for Cyanobacteria

Lytic Bacterial Genera	References
Actinomyces	Safferman and Morris, 1962 Sladekova and Sladek, 1968
Streptomyces	Gunnison and Alexander, 1975
Bacillus	Reim *et al*., 1974
Pseudomonas	Mitchell, 1972
Cellvibrio	Granhall and Berg, 1972
Bdellovibrio	Burnham *et al*., 1976
Myxobacteria	Stewart and Brown, 1971; Wu *et al*., 1968; Daft and Stewart, 1971;1973; Daft, McCord and Stewart, 1975; Shilo, 1970
Cytophaga	Stewart and Brown, 1969
Myxococcus	Burnham, et al. 1979; 1980 a, b

production of enzymes during its life cycle processes of fruiting body and cyst formation (Kottel and White, 1974).

Wu _et_ _al_. (1968) indicated that an unidentified myxobacterium was capable of lysing in a liquid culture strain of _Lyngbya_ and five other blue-green species. The authors indicated that lysis was associated with a slow "clumpy" growth of the myxobacterium and the production of a lysin.

Stewart and Brown (1969) isolated a _Cytophaga_ which formed plaques on both green and blue-green algae. These authoris indicated that the lysis of the algae was extracellular, but the exact cause of lysis was not described.

Shilo (1970) isolated a myxobacter (designated FP-1) that lysed viable vegetative cells of many unicellular and filamentous blue-green algae. Lysis in liquid cultures was prevented when the algal cultures were shaken. Light microscopy demonstrated that algal lysis only occurred upon polar attachment of the myxobacter to the algal cell. Detection of excreted lytic enzymes was unsuccessful, suggesting that the lytic enzymes may be bound to the surface of the myxobacter.

Five algicidal non-fruiting myxobacteria were described by Stewart and Brown (1971) to have a uniformly high G+C ratio of approximately 70 mole percent. All of these organisms were effective in lysing algae but none of these bacteria were capable of forming microcysts, a feature which distinguishes them from the _Myxococcus_ PC02 isolate. Myxobacter has been a general name for any bacterium falling within two orders, Myxobacteriales and Cytophagales. Using the criteria described by Stewart and Brown (1971), their isolates would be grouped as members of the _Cytophaga_ genus by the 9th edition of Bergeys Manual (Buchanan and Gibbons, 1974).

Daft and Stewart (1971) described four myxobacters that could lyse 40 strains of blue-green algae. Again cell contact appeared to be necessary for lysis to occur. The authors suggested that one bacterium can initiate lysis of the algae. Although lysis took from 2 to 7 days, photosynthesis was inhibited about 85% after 10 hours. Daft and Stewart (1971) indicate that these myxobacteria may be important in regulating algal development in nature.

The structural basis for algal lysis by the Myxobacterium CP-1 was described by Daft and Stewart (1973). The primary ultrastructural effect was the dissolution of the L2 or mucopeptide layer in the cell wall of the blue-green algae tested. Large intrathylakoidal spaces were seen to form; however, the membranes themselves seemed very resistant to myxobacter CP-1 disruption. This pathology of the photosynthetic system is very similar to that described for bdellovibrio interaction with _Phormidium_ _luridum_ (Burnham and Sun, 1977). Daft and Stewart (1973) point out that the concentration of bacteria employed in these structural studies were far in excess of those encountered in nature. Generally, a 1:1 proportion of bacteria with algae were employed in their studies.

The physiologic conditions under which algal lysis by various myxobacteria occurred was reported by Daft _et_ _al_. (1975). The lytic bacteria were all strict aerobes. Lysis increases as the CO_2 was increased to 45%. Higher levels were inhibitory. The pH optima for lysis was within the range of 7.0 to 9.0 for all strains of myxobacteria tested.

Lysis was not reported at 37°C for strain CP-1. Daft _et_ _al_. (1975) suggest that optimum lysis in the field should be expected in the summer months in shallow water as the pH will also be quite suitable. The number of myxobacteria per ml of lake water ranged from 4 to 400. These authors showed that in surveying 8 bodies of water in Scotland (5 lakes, 2 reservoirs and 1 sewage plant), there was always a direct statistical correlation between chlorophyll a concentration in the water and the abundance of these lytic bacteria.

The report by Burchard (1975) of colonial spherule formation by M. xanthus in axenic culture provided significance to the feasibility of myxococci as a biological control agent. It conclusively demonstrated that the myxococci possessed a capability for orderly aggregation in liquid environments. This was important in view of their earlier established aggregative properties on semi-solid media (Dworkin, 1973).

MYXOCOCCAL CYANOBACTERIAL ENTRAPMENT AND LYSIS

A Myxococcus xanthus designated PC02 was isolated in Port Clinton, Ohio, from a roadside ditch that evinced excellent lysis on agar grown lawns of cyanobacteria. When the organism was tested in aqueous cultures of Phormidium luridum, a filamentous cyanobacterium, I found that the cyanobacteria became clumped, overgrown by the myxococci and finally lysed. Although much of the research has been recently reported (Burnham et al., 1979; 1980a; 1980b), I would like to review the major characteristics of this lytic system in this presentation.

The antagonism of M. xanthus PC02 toward the cyanobacterium P. luridum is clearly illustrated in Figs 1 and 2. Figure 1 shows that upon repeated transfer in an autotrophic medium, the cyanobacterium alone was always capable of multiplying sufficiently to prevent being diluted out. The P. luridum plus myxococci under similar autotrophic conditions, however, was not capable of multiplying and the 5% transfers rapidly diluted out the cyanobacteria to undetectable levels. Figure 2 shows that upon extended coincubation the myxococci can effectively lyse large numbers of cyanobacteria and maintain the environment at a reasonably low level of cyanobacterial cells per ml. Some cycling of the culture is periodically observed. The P. luridum are able to multiply by several logs; however, this increased growth is again soon lysed by the residual myxococci. This cycling demonstrates the inability of the M. xanthus PC02 system to completely remove all cyanobacteria from the environment. Significantly, I have found that lysis of a culture can be accomplished with predator to prey ratios of 1:100,000. This is significant in view of the need to be able to use low inocula in natural ecosystems if practical usage is to ensue.

Figure 3 shows the ability of the M. xanthus PC02 strain to lyse P. luridum on agar lawns. The photograph further demonstrates the spreading or gliding motility that the myxococci possess. These myxococci are normally maintained on lawns of prey cyanobacteria as it ensures that the predatory ability will be retained and even increased as a result of selection of the cells most rapidly clearing the cyanobacteria.

The initial clumping that occurs shortly following the addition of the myxococci to a cyanobacterial culture develops over 12 to 24 hrs into very distinct colonial spherules. With low magnification phase contrast microscopy (Fig. 4) it can be observed that the spherule is made up of an outer region and a core. If the photograph were in color, it would be apparent that the outer region was yellowish while the core was a dense green. The spherule is able to concentrate the cyanobacteria into the central regions of the spherule as demonstrated by thin-sectioning the spherules and examining the core by transmission electron microscopy (Burnham et al., 1979; 1980b). Mature colonial spherules often reach a diameter between 1 to 5 mm.

When axenic spherules of myxococci alone are examined using parafin embedment and light microscopy, the separation of core and myxococcal growth at the surfaces of the spherule is very clear (Figure 5). High

1

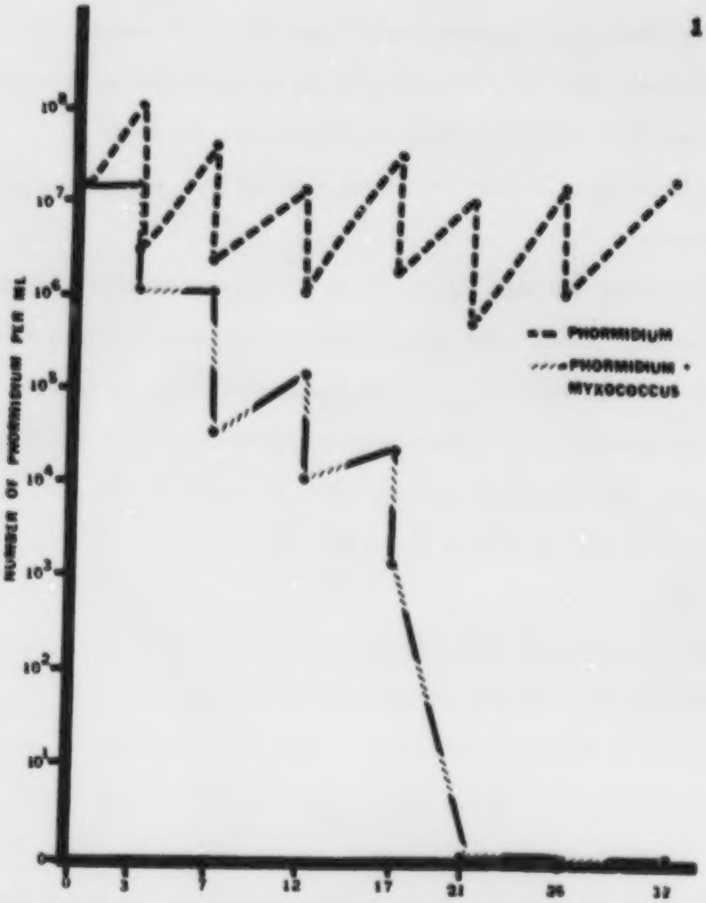


Figure 1. This graph illustrates the result of repeated 5 percent serial transfers (indicated by the vertical lines) on axenic cultures of the cyanobacterium *P. luridum* and an interactive mixture of washed *M. xanthus* PC02 ($1x10^6$ cells/ml) and *P. luridum* ($2x10^7$ cells/ml) into a fresh flask of algae broth (Difco). As can be seen from the upper dashed lines, when the *P. luridum* cells alone were transferred, they multiplied back to approximately original levels. When the coincubated microorganisms were transferred, the *M. xanthus* PC02 prevented this multiplication of the *P. luridum* so that within five transfers the cyanobacteria were not detectable by microscopic counting procedures.

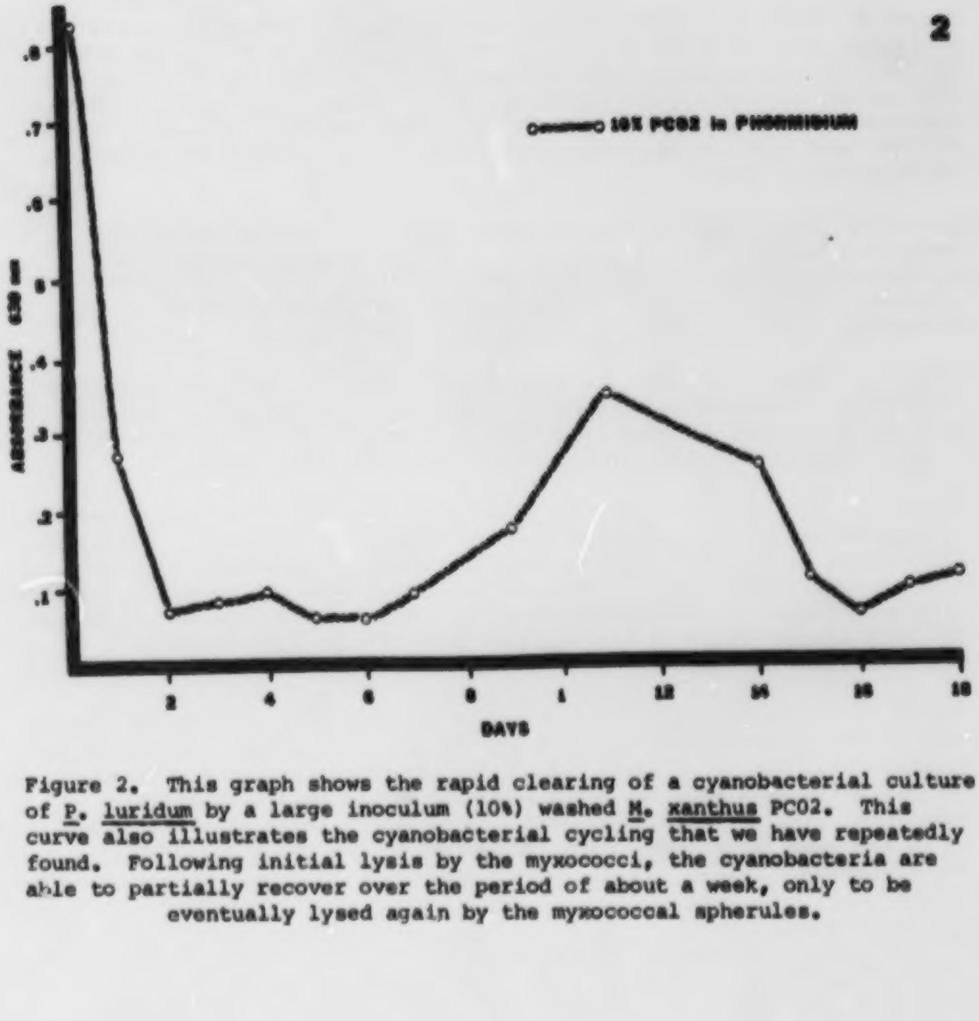


Figure 2. This graph shows the rapid clearing of a cyanobacterial culture of P. luridum by a large inoculum (10%) washed M. xanthus PC02. This curve also illustrates the cyanobacterial cycling that we have repeatedly found. Following initial lysis by the myxococci, the cyanobacteria are able to partially recover over the period of about a week, only to be eventually lysed again by the myxococcal spherules.

Figure 3. Macrophotograph of an algae agar-containing petri plate upon which a mature lawn of the cyanobacterium, *P. luridum* (darker region) has been grown. An agar block containing *M. xanthus* PC02 was placed in the center of the mature lawn. The concentric spreading cyanobacterial lysis caused by the gliding myxococci can be seen in the clear circular zone on the plate. The rectangular zone at the edge of this circle is where an agar block was removed and transferred to another cyanobacterial lawn. This degree of lysis is commonly seen after 5 to 7 days. Magnification: 0.9X.

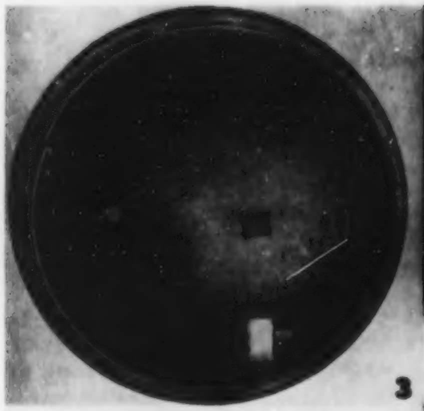
Figure 4. This is a phase contrast micrograph of a partially compressed *M. xanthus* PC02 spherule containing the cyanobacterium *M. xanthus* PC02 in the core (dense) region. Also present in the core are numerous crystals that appear to have a function in the flocculation in the early stages of spherule formation. At the spherule's surface numerous myxococcal cells diffuse away from the spherule as a result of the compression technique. Magnification: 180X.

Figure 5. This bright field macrograph shows a Gram-stained paraffin embedded spherule of *M. xanthus* PC02. The outer dense growth of the myxococcal cells is apparent as is the relatively unstructured core (lighter) region. The significance of the intermediate banding by the myxococcal cells has not been determined. Magnification: 315X.

Figure 6. This phase contrast micrograph shows a filament of *P. luridum* completely surrounded by vegetative cells of *M. xanthus* PC02. The filament is in the early stages of degradation as evinced by the separation of the filament into individual cells. Magnification: 1020X.

Figure 7. This scanning electron micrograph shows the parallel orientation of many of the myxococcal cells on the surface of a spherule. The larger filamentous *P. luridum* protrudes from the surface in several locations. Also noticable are ridges on the surface of the spherule formed by hundreds of the myxococci in parallel orientation. These are postulated to be due to the swarming action of the myxococi over the spherule surface. Magnification: 2650X.

Figure 8. This scanning electron micrograph shows the rod-like *M. xanthus* PC02 cells joined together by small fiberlike protrusions. Transmission electron microscopy confirmed that these are composed of lipopolysaccharide and are contiguous with the outer membrane of the cell wall of the myxococcal cells. The entanglement of the fibers holds the sphere into shape and suggests a role of the entrapment of the cyanobacteria. Magnification: 7015X.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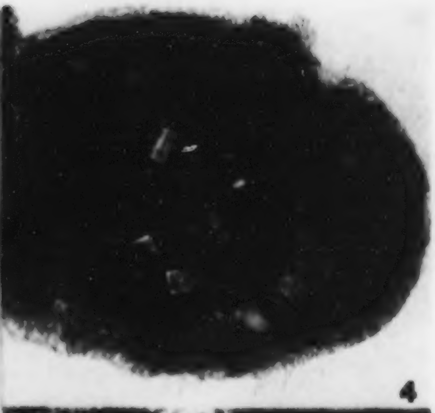
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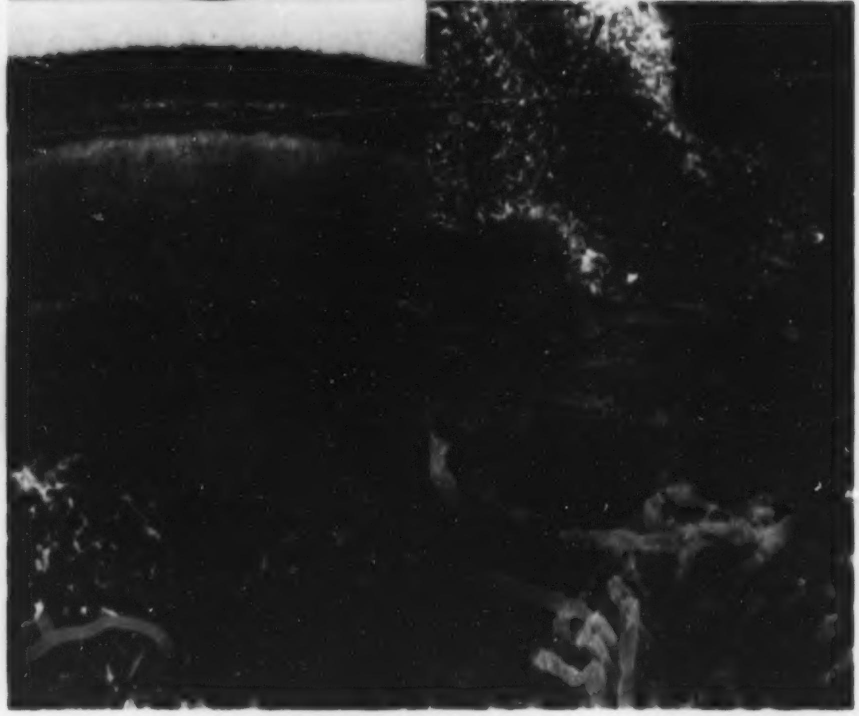

magnification phase contrast microscopy of a young spherule (Figure 6) shows the large numbers of myxococci surrounding an entrapped P. *luridum* filament which is in the process of being degraded by myxococcal enzymes. Because the spherules increase in size with age and addition of cyanobacterial prey, and because the entire system operates under autotrophic conditions, the cyanobacteria must be serving as nutrient for myxococcal growth.

Closer examination of the surface of the colonial spherule by scanning electron microscopy (Figure 7) shows a distinct orientation of the myxococcal cells with several of the larger cyanobacterial filaments protruding from the spherule surface. Dworkin (1973) and Kaiser *et al*. (1979) have shown that the myxococci are aggregative bacteria that often swarm over a surface in the process of organizing the colony for production of fruiting structures. I postulate that myxococcal swarming is both the process responsible for the parallel orientation of the bacteria at the surface of the spherule and the primary mechanism by which the myxococci concentrate the cyanobacteria in the spherule core. By constantly gliding over the outer regions of the spherule, the myxococci cover the cyanobacteria, and by continual myxococcal shifting the cyanobacteria are gradually deposited in the core.

Figure 8 shows the stringy protrusions of lipopolysaccharide (Burnham *et al*., 1980b) that tie the spherule together. These plus the fimbriae that have been demonstrated by Dobson and McCurdy (1979) also appear to serve as tentacles assisting in the entrapment of cyanobacteria from the surrounding medium.

Finally, I believe the lysis of the cyanobacterial cells within the spherule core occurs because of the well described exoenzymes produced by the myxococci.

MYXOBACTERIAL LYTIC ENZYMES

In studying the myxobacter strain AL-1, Ensign and Wolfe (1965) described an enzyme possessing both proteolytic and cell wall lytic activity. These two functions were inseparable upon purification.

Hart and Zahler (1966) studied a lysin produced by *M. xanthus* FBa. Purification yielded two distinct enzymes, a lysozyme and a protease. The lysozyme was very effective in lysing cell walls of various microorganisms.

Further purification of *M. xanthus* FB bacteriolytic enzyme was described by Sudo and Dworkin (1972). BY gel separation techniques an amidase, a glucosaminidase, two proteases with amidase activity and a peptidase active against cell wall peptides were isolated. These are all individually capable of bacteriolytic activity and collectively they appear to indicate why the *Myxococcus* and its related genera are such potent antimicrobial parasites.

Haska (1974) purified the peptidase produced by a related species, *M. virescens*, and identified it to be a D-alanyl-N lysine endopeptidase, an enzyme that would cause the destruction of the L2 (mucopeptide) layer as observed by Daft and Stewart (1973).

An alternative mechanism for the lysis of algal species could relate to the autolytic system that has been described for *M. xanthus* FB (Kottel and White, 1974). This enzyme system is induced during myxocyst formation. The release of these enzymes which appear to result in the dissolution of cell walls could lyse walls of sensitive cyanobacterial strains. Wireman and Dworkin (1977) further characterized this autolysis in terms of its sequence in the morphogenic events leading to myxocyst development. The formation of the myxocyst appears to be dependent on the cell-free concentration of cytoplasmic constituents from lysed myxococci. This necessity for lysis of a certain percentage of the total myxococcal population provides the rationale for the autolytic mechanism.

Myxococcus xanthus strains have been shown to also produce an antibiotic active against both Gram-positive and Gram-negative bacteria. The antibiotic appears to be bacteriocidal. *Escherichia coli* B cells, when exposed to this myxococcal antibiotic for 60 min,all showed lysis (Rosenberg *et al*., 1973). Vaks *et al*. (1974) characterized the antibiotic to be active only against growing cells.

Finally, it has been reported recently that certain proteases are bound to the extracellular slime found associated with *M. virescens* B2 (Gnosspelius, 1978). The author suggests that these enzymes could play an important role in denaturing protein components from microbial prey cells lysed by myxobacterial activities.

SUMMARY AND RECOMMENDATIONS

The *M. xanthus* colonial spherules, to the extent they have been tested in my laboratory, offer excellent potential as microbial control agents for cyanobacteria. The specific advantages of these lytic mechanisms are listed in Table 3. Heading the list is the primary reason why I am enthusiastic about this lytic system; i.e., it is capable of fuctioning in the total absence of heterotrophic nutrient other than aqueous cyanobacteria. This is in complete contrast to the *Bdellovibrio bacteriovorus* system previously described (Burnham *et al*., 1976b)which requires a high concentration of exogenous protein in order to function. Also distinctive is the ability to carry out cyanobacterial lysis at high agitation rates. This is due to the confined nature of the lytic system and the ability of the *M. xanthus* to swarm over the cyanobacteria, thereby moving them to the core regions. The encystment ability of the *M. xanthus* species allows predator survival in periods of adversity such as winter or reduced availability of cyanobacterial hosts. Although Daft *et al*. (1975)

found a significant reduction in myxobacterial predator counts in the winter versus summer in Scottish waters, they did at least document the survival of the predator species. My laboratory has successfully tested 7 strains of cyanobacteria for prey status. This plus the results of Daft and Stewart (1971) indicating that the major cyanobacterial bloom producers (ex. Aphanizomenon flos-aquae; Microcystis aeruginosa; Anabaena circinalis; A. spiroides and Caelosphaerium) were all lysed by myxobacteria further heighten the control potential for this type of bacterium. Following continued monitoring of various environmental parameters and larger scale testing in tanks, I hope to develop a testing program utilizing controlled pond situations.

The various viewpoints presented at this conference suggest a series of recommendations with regard to microbiological control system development: (a) The data produced in my own laboratory and that from the other research cited in the review, particularly that of Daft et al. (1975), indicates microbial control has a potential value to the management of cyanobacteria in lakes and reservoirs; (b) With the increasing costs associated with lake management that this conference has demonstrated it appears that the favorable cost/benefit ratio that could be provided by biological control only increases the need for successful development of a microbial control system; (c) With the need for an effective microbiological control system evident, funding agencies should approach various disciplines, not only microbiology, with "requests for proposal" to develop more innovative ideas in this field (One significant accomplishment of the conference was to bring together experts from many disciplines and the resultant exchange was very stimulating. Such an approach could work in funding new research.); (d) A funding agency might utilize the multidisciplinary approach to review projects as well, and if an idea appeared collectively successful to a multidisciplinary lake or water management group, it could be given increased priority over traditional reviews; (e) Research in the field of microbial control needs to be

TABLE 3

Advantages of the *Myxococcus xanthus* lytic spherules as a microbial biological system

1. effective in autotrophic environment
2. utilization of dominant microorganisms as nutrient in eutrophic aquatic systems
3. low inoculum of predator effective
4. independent of environmental agitation
5. non-specific host requirement
6. effective host entrapment mechanism
7. lytic system contained and segregated
8. multicomponent nature of lytic system
9. encystment ability of predator
10. predator survival in hostile environments

simultaneously (1) developed in order to understand the nature of the biochemical structural interactions that occur between predator and prey and (2) evaluated in increasingly complex systems which progressively mimic the natural ecosystems that are targeted; (f) The funding mechanism should include sufficient commitment to provide testing in controlled natural ecosystems such as test pond environments; (g) Successful programs should be integrated with other physical and biological techniques into a well-monitored lakes management program.

The establishment of such a program could bring about the improvement in water quality we all desire in a manner consistent with the challenge to avoid further toxification or pollution of the aquatic ecosystem.

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REFERENCES

Beebe, J. M. 1941. Studies on the Myxobacteria. 2. The role of Myxcbacteria as bacterial parasites. Iowa State J. Sci. *15*:319-337.

Buchanan, R. E., and N. E. Gibbons (eds.). 1974. Bergey's Manual of Determinative Bacteriology. 8th Edition. The Williams and Wilkins Company, Baltimore.

Burchard, R. 1975. Myxospore induction in a nondispersed growing mutant of *Myxococcus xanthus*. J. Bacteriol. *122*:301-306.

Burnham, J. C. 1975. Bacterial control of aquatic algae. *In* the Proceedings of a Symposium on Water Quality. Management through Biological Control. Gainesville, Florida.

Burnham, J. C., G. Locher and D. C. Sun. 1976a. An ultrastructural analysis of photosynthetic stress in the cyanobacteria, *Phormidium luridum* and *Microcystis aeruginosa*. Abs. Ann. Mtg. Am. Soc. Microbiol. I113.

Burnham, J. C., T. Stetak, and G. Locher. 1976b. Extracellular lysis of the blue-green algae *Phormidium luridum* var. *olivacea* by *Bdellovibrio bacteriovorus*. J. Phycol. *12*:306-313.

Burnham, J. C. 1977. Bacterial control of aquatic algal populations. Project Completion Report 548. U. S. Dept. of Interior.

Burnham, J. C., and D. Sun. 1977. Electron microscope observations on the interaction of *Bdellovibrio bacteriovorus* with *Phormidium luridum* and *Synechococcus* sp. (Cyanophyceae), J. Phycol. 11:203-208.

Burnham, J. C., S. A. Collart and B. Highison. 1979. Entrapment and lysis of *Phormidium luridum* by colonial spherules of a *Myxococcus* species. Abs. Ann. Mtg. Am. Soc. Microbiol. 120.

Burnham, J. C., S. A. Collart and B. Highison. 1980a. Myxobacterial antagonism for *Phormidium luridum*. Abs. Ann. Mtg. Am. Soc. Microbiol. p.85(I6)

Burnham, J. C., S. A. Collart and B. W. Highison. 1980b. Entrapment and lysis of the cyanobacterium *Phormidium luridum* by colonial spherules of *Myxococcus xanthus* PCO2. Arch. Microbiol. (submitted for publication).

Daft, J. J., S. B. McCord, W. D. P. Stewart. 1975. Ecological studies on alga-lysing bacteria in fresh waters. Freshwat. Biol. 5:577-596.

Daft, J. J., and W. D. P. Stewart. 1971. Bacterial pathogens of freshwater bluegreen algae. New Phytol. 70:819-829.

Daft, M. J., and W. D. P. Stewart. 1973. Light and electron microscope observations on algal lysis by bacterium CP-1. New Phytol. 72:799-808.

Dobson, W. J., and H. D. McCurdy. 1979. The function of fimbriae in *Myxococcus xanthus*. 1. Purification and properties of *M. xanthus* fimbriae. Can. J. Microbiol. 25:1152-2260.

Dworkin, J. 1973. Cell-cell interactions in the myxobacteria. In Microbial Differentiation, Ashworth, J. M., Smith, J. E., eds., 23rd Symp. Soc. Gen. Microbiol., Cambridge Univ. Press, London, pp. 125-142.

Ensign, J. C., and R. S. Wolfe. 1965. Lysis of bacterial cell walls by an enzyme isolated from a myxobacter. J. Bacteriol. 90:395-402.

Fallon, R. D., and T. D. Brock. 1979. Decomposition of bluegreen algal (cyanobacterial) blooms in Lake Mendota, Wisconsin. Appl. Env. Microbiol. 37:820-830.

Fitzgerald, G. P. 1969. Some factors in the competition or antagonism among bacteria, algae, and aquatic weeds. J. Phycol. 5:351-359.

Fogg, G. E. 1952. The production of extracellular nitrogenous substances by a blue-green algae. Proc. R. Soc. London. Ser. B. 139:372-397.

Fogg, G. E., W. D. P. Stewart, P. Fay and A. E. Walsby. 1973. The blue-green algae. Academic Press, N. Y.

Gnosspelius, G. 1978. Purification and properties of an extracellular protease from Myxococcus virescens. J. Bacteriol. 133:17-25.

Granhall, U. and B. Berg. 1972. Antimicrobial effects of Cellvibrio on blue-green algae. Arch. Mikrobiol. 84:234-42.

Gunnison, D. and M. Alexander. 1975. Basis for the susceptibility of several algae to microbial decomposition. Can. J. Microbiol. **21**:619-28.

Hart, B. A. and S. A. Zahler. 1966. Lytic enzyme produced by *Myxococcus xanthus*. J. Bacteriol. **92**:1632-1637.

Haska, G. 1974. Extracellular lytic enzymes of *Myxococcus virescens*. IV. Purification and characterization of a D-alanyl-e-N-lysine and endopeptidase. Physiol. Plant. **31**:252-256.

Huffaker, C. B. and P. S. Messenger. 1976. *Theory and Practice of Biological Control*. Academic Press, New York.

Kaiser, D., C. Manoil, J. Dworkin. 1979. Myxobacteria: cell interactions, genetics and development. Ann. Rev. Microbiol. **33**:595-639.

Kottel, R., and D. White. 1974. Autolytic activity associated with Myxospore formation in *Myxococcus xanthus*. Arch. Microbiol. **95**:91-95.

Lang, N. J. 1968. The fine structure of the blue-green algae. Ann. Rev. Microbiol. **22**:15-46.

Lange, W. 1970. Cyanophyta-bacteria systems: effects of added carbon compounds or phosphate on algal growth at low nutrient concentrations. J. Phycol. **6**:230-234.

Lange, W. 1971. Enhancement of algal growth in cyanophyta-bacteria systems by carbonaceous compounds. Can. J. Microbiol. **17**:303-314.

Mitchell, R. 1972. Water Pollution Microbiology. Wiley-Interscience, New York.

Paerl, H. W. 1976. Specific associations of the bluegreen algae *Anabaena* and *Aphanizomenon* with bacteria in fresh water blooms. J. Phycol. 12:431-435.

Reim, R. L., M. S. Shane and R. E. Cannon. 1974. The characterization of a *Bacillus* capable of blue-green bactericidal activity. Can. J. Microbiol. 20:981-986.

Rosenberg, E., B. Vaks, and A. Zuckerberg. 1973. Bactericidal actions of an antibiotic produced by *Myxococcus xanthus*. Antimicrobial Agents and Chemotherapy. 4:507-513.

Safferman, R. A. and M. E. Morris. 1962. Evaluation of natural products for algicidal properties. Appl. Microbiol. 10:289-292.

Shilo, M. 1967. Formation and mode of action of algal toxins. Bacteriol. Rev. 31:180-193.

Shilo, M. 1970. Lysis of bluegreen algae by Myxobacter. J. Bacteriol. 104:453-461.

Sladeckova, A. and V. Sladeck. 1968. Algicides---friends or foes? In Algae, Man and the Environment. pp. 441-458. Syracuse University Press, New York.

Stewart, J. R. and R. M. Brown. 1969. Cytophaga that kills and lyses algae. Science. 164:1512-1524.

Stewart, J. R., and R. M. Brown, Jr. 1971. Algicidal non-fruiting Myxobacteria with high G+C ratio. Arch. Mikrobiol. 80:176-190.

Sudo, S., and M. Dworkin. 1972. Bacteriolytic enzymes produced by Myxococcus xanthus. J. Bact. 110:236-245.

Vaks, B., A. Zuckerberg and E. Rosenberg. 1974. Purification and partial characterization of an antibiotic produced by Myxococcus xanthus. Can. J.Microbiol. 20:155-161.

Wireman, J. W., and M. Dworkin. 1977. Developmentally induced autolysis during fruiting body formation by Myxococcus xanthus. J. Bact. 129:796-802.

Wu, B., M. K. Handy, and H. B. Howe, Jr. 1968. Antimicrobial activity of a myxobacterium against blue-green algae. Bacteriol. Proc. GP14.

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G. W. Prescott
Emeritus Professor of Botany
University of Montana

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BIBLIOGRAPHY

1. Anonymous. (Undated). Controlling plant and animal pests in farm ponds with copper sulphate. Phelps Dodge Refining Corp. Bull.

2. Anonymous. 1904. The use of copper sulphate as an algicide at Cambridge. New York Eng. News 52: 53.

3. Anonymous. 1924. Copper sulphate treatment of algae troubles. Jour. Amer. Water Works Assoc. 11: 258-265.

4. Anonymous. 1925. How the effect of copper sulphate on algae was discovered. Eng. Contract. 64: 283.

5. Anonymous. 1925. Applying copper sulphate. Eng. Contract. 63: 125-126.

6. Anonymous. 1929. Algae in water supply control by chlorination. Municip. Eng. Sanita. Rec. 83: 526.

7. Anonymous. 1936. Suggestions for preventing algal growth in water supply reservoirs. Eng. Contract. Rec. 50: 21.

8. Anonymous. 1939. A study of silt on absorbing light which promotes the growth of algae and moss in canals. U.S. Dept. Inter. Bur. Reclam., Washington, D.C.

9. Anonymous. 1939. Report on the chemical treatment of lakes and streams with special reference to the origin and control of swimmers itch. State of Wisconsin Comm. on Water Pollution, Madison. 20 pp.

10. Anonymous. 1942. Copper sulphate for aquatic nuisances. Public Works 73(9): 21, 47.

11. Anonymous. 1943. Plankton growths cause difficulties at Hamilton. Eng. Contract. Rec.

12. Anonymous. 1944. The D. N. (Monie-$CuSO_4$) test. Rep. West Virginia Pulp & Paper Co., New York.

13. Anonymous. 1947. A report on algae control in fish hatchery tanks. Unexcelled Chem. Corp. Bull., New York.

14. Anonymous. 1950. Water quality and treatment. Amer. Water Works Assoc. Chap. 5, pp. 1-451. (101-124).

15. Anonymous. 1951. Revised list of bulletins and leaflets on Ohio fishes and related subjects. Ohio Dept. Nat. Resources, Div. of Wildlife.

16. Anonymous. 1951. Bromine for slime and algae control. The Betz Indicator 20(6): 2-4; 7,8.

17. Anonymous. 1951. Removing algae and slime. Golf Course Rep. 19(2):40.

18. Anonymous. 1951. Algae killer. Chem. & Eng. News 29(5): 356.

18a. Anonymous. 1952-1953. Fisheries research--weed control experiments. State of Alabama, Dept. Conserv., Rep. for fiscal year 1952-53, pp. 115, 116.

19. Anonymous. 1952. Purer ponds. Chem. Age 66(1708): 497.

20. Anonymous. 1953. Algae growth in wooden cooling towers. Angew. Chem. 65(3). (Potassium chromate).

21. Anonymous. 1954. Control of bloom-producing algae. Bethany Informa. Sheet 75. 2 pp. U.S. Rubber Co., Naugatuck Chem. Div.

22. Anonymous. 1954. Control of algae in ponds. Univ. Kentucky Exper. Station, 66th Ann. Rep. p. 47.

23. Anonymous. 1963. Treatment of cold-weather algae. Water & Sewage Works 110: 229.

24. Anonymous. 1965. New ways to apply aquatic herbicides. Weeds, Trees and Turf 4(2): 18, 19; 24, 25; 4(4): 18-20.

25. Anonymous. 1968. Trends and discoveries. Cleaning lakes of algal blooms. New Scientist 40: 385.

26. Anonymous. 1969. Swedes find a virus that attacks algae. New Scientist 44: 278.

27. Adams, B. A. 1927. The lethal effects of various chemicals on *Cyclops* and *Daphnia*. Water Works Eng. 29: 361-364.

28. Adamson, R. P. and Sommerfeld, M. R. 1977. Swimming pool algae and their chemical control in Phoenix metropolitan area. Arizona, USA. Jour. Phycol. 13(Suppl.): 3.

29. Agersborg, H. P. K. and Hatfield, W. D. 1929. The biology of a sewage treatment plant--a preliminary survey. Decatur, Illinois. Sewage Works Jour. 1(4): 411-424.

30. Allen, C. K. 1966. Use of copper sulphate in water treatment. Water & Sewage Works 113: R71, R72, R74, R75.

31. Allen, S. E. and Skoog, F. 1951. Phytotoxicity of imidazoline and related compounds. Plant Physiol. 26: 611-

32. Almquist, E. 1959. Observations on the effect of rotenone emulsives on fish food organisms. Inst. Freshwater Res., Drottningholm, Rep. 40: 146-160.

33. Anderson, H. F. 1954. Out with algae: Eau Claire, Wis. clears up a lake problem with copper sulphate. American City 69: 118, 119.

34. Anders, W. W. 1961. Two-point copper sulphating program licks algae problems. Water Works Eng. 114: 700, 701, 729, 732.

35. Angell, H. H. 1953. Rout reservoir algae in winter. American City 68(10): 90, 91.

36. Anthony, S. S. 1947. Copper sulphate distributor. Jour. New England Water Works Assoc. 61: 253-259.

37. Anthony, S. S. 1948. A copper-sulphate distributing craft. Water & Sewage Works 95(Ref. & Data Sec.): R151.

38. Antonides, H. J. and Dietchweiler, R. L. 1965. Algicidal and sanitizing composition. U.S. Patent 3,201,311.

39. Antonides, H. J. and Tanner, W. S. 1961. Algicidal and sanitizing properties of Armazide. Appl. Microbiol. 9: 572.

40. Arasaki, S. and Nozawa, K. 1958. An algicide, Delrad 70. Bull. Jap. Soc. Sci. Fish. 23: 599-603.

41. Arlee, H. F. 1956. Aquatic weeds: submersed and emergent. The effect of several herbicides on algae. Res. Progr. Rep. Western Weed Control Confer. 1956, pp. 83, 84.

42. Arnold, G. E. 1936. Plankton and insect larvae control in California waters. Jour. American Water Works Assoc. 28: 1469-1479.

43. Bado, A. A. 1920. La eficacia del sulfato de cobre par a la destruccion de algas in las aquas potables. Anales Soc. Quim. Argentina 8: 14-17.

44. Bailey, W. T. 1929. Electrolytic chlorine for the destruction of algae. American City 40: 103.

44a. Bailey, W. T. 1935. Taste and odor control at Council Bluffs. Jour. American Water Works Assoc. 27: 458-471.

45. Bailey, W. T. 1942. The use of activated carbon for preventing the growth of algae in open mixing and settling basins. In: Taste & Odor Control in Water Purification. Indus. Chem. Sales Div., West Virginia Pulp & Paper Co., New York.

46. Baker, M. N. 1949. The quest for pure water. In: Algal troubles and their conquest. Jour. American Water Works Assoc., pp. 391-414.

47. Bakke, O. M. 1926. Chloro tastes and their eradication at Dallas, Texas. Jour. Amer. Water Works Assoc. 16: 730-736.

48. Baldwin, H. B. and Whipple, G. C. 1906. Observed relation between dissolved oxygen, carbonic acid and algae growths in Weequahic Lake, N.J. Rep. American Health Assoc. 32: 167-182.

49. Barbehenn, K. 1954. The effects of ducks on the development of filamentous algae in farm fishponds. N. Y. Fish & Game Jour. 1(1): 110-115. (Natural control)

50. Bartholomew, K. A. 1958. Control of earthy, musty odors in water by treatment with residual copper. Jour. American Water Works Assoc. 50: 48.

51. Bartsch, A. F. 1946. Aquatic nuisance control in Wisconsin. Comm. on Water Pollution. Madison, Wisconsin.

52. Bartsch, A. F. 1954. Practical method for control of algae and water weeds. American Public Health Rep. 69(8): 749-757.

53. Bartsch, A. F. 1955. Practical methods for control of algae and water weeds. Public Works 86(2): 86, 87; 144-146.

54. Bartsch, A. F. 1970. Eutrophication: a threat to water resources. Symposium on Hydrobiology-Bioresources of shallow water environment, Miami, Florida 1970. pp. 127-135.

55. Basset, H. S. 1955. Treatment of water with magnesium and sulfur dioxide. U.S. Patent 2,728,726: (Chem. Abstr. 50: 8110a).

56. Bean, E. L. 1935. Providence water treatment. Jour. New England Water Works Assoc. 49(4): 406-418.

57. Bean, E. L. 1957. Taste and odor control at Philadelphia. Jour. American Water Works Assoc. 49(2): 205-216.

58. Beddow, D. G., Schlichting, H. E. and Vance, B. D. 1968. The survival of some algae in highly chlorinated water. Advanc. front. Plant Sci. 19: 165-178.

59. Benckiser, J. A. 1962. Protective agents against the settling of microorganisms, and against fungi, algae, protozoa and insects. Jour. Sci. Food Agric. 13: 1-302.

60. Bentlry, W. 1957. Public relations in aquatic plant and algae control. (Paper read at Northeastern Weed Control Confer. 1957).

61. Berens, W. 1954. Exit algae! Park Maintenance 1954: 26, 28.

62. Berry, A. E. 1942. How to handle alga problems. Aquatic growths, particularly troublesome in Ontario this year. Canadian Eng. 80: 9.

63. Berry, A. E. 1961. Removal of algae by microstrainers. Jour. American Water Works Assoc. 53: 1503-1508.

64. Bervoets, W. P. 1952. De l'effet de l'hexachlorocyclohexane sur la plancton. Hydrobiologia 4: 214-219.

65. Betant, A. 1918. Action of copper sulphate on plankton. Arch. Sci. Phys. Nat. 46(Suppl.): 86-91.

66. Betz, W. H. and Betz, L. D. 1955. Slime and algae control. Betz Indicator 20(6): 2-4.

67. Betz, W. H. and Betz, L. D. 1955. Slime and algae control. Betz Indicator 24(5): 2-8.

68. Betzer, N. and Knott, Y. 1969. Effect of halogens on algae. II. Cladophora sp. Water Res. 3: 257-264.

69. Billings, L. C. 1936. Tastes and odors--causes and prevention. Proc. 18th Ann. Texas Water & Sewage Works Short School, 1936.

70. Billings, L. C. 1942. Taste and odor control in the treatment of surface waters. Proc. 24th Ann. Texas Water & Sewage Works, Short School, 1942.

71. Birmingham, B. C. and Colman, B. 1977. The effect of 2 organo phosphate insecticides on the growth of fresh water algae. Canadian Jour. Bot. 55(11): 1453-1456.

72. Birrer, A. 1935. Aktives Chlor und seine Einwirklung auf niedere Wasserorganismens. Zeit. f. Hydrobiol. 1933: 64-104.

73. Black, J. D. 1946. Nature's own weed killer, the German carp. Wisconsin Conserv. Bull. 11: 3-7.

74. Bohdanova, T. L. 1962. Possible control of algae by chemical means; preliminary report. Visn. Kiivsik Univ., Ser. Biol. 5, 10(3):

75. Borasio, L. 1952. Le probleme de la tutte contre les algues. Jour. de Riz 1952: 99-101.

76. Borasio, L., De Rege, F. and Girardi, A. 1953. Chemical control of algae--a new product called "disalgon". Colt. e Gior. Vinic. Ital., II, 99: 81-84.

77. Boschetti, M. M. 1957. A study in the chemical control of aquatic vegetation. Sanitalk 5(2): 31-35.

78. Bouilhac, R. 1894. Influence de l'acide arsenique sur la vegetation des algues. Compt. Rend. Acad. Sci. Paris 119(22): 929-931.

78a. Bowser, C. W. 1951. Rada for algae. The Reclamation Era 37: 247-248.

79. Boyer, B. B. 1947. Aquatic weed control manual. The Chloroben Corp., Jersey City, N.J.

80. Braginskii, L. P. 1964. Application of the oxygen method in algotoxic investigations. Gidrobiol. Acad. SSR, Zoological Inst. 1964: 108-116.

81. Braginskii, L. P., *et al*. 1963. Monuron and simazine as algicides. Tr. Vses Gidrobiol. Obschestva Akad. Nauk SSSR 14: 52-65.

82. Brannon, M. A. and Bartsch, A. F. 1939. Influence of growth substances on growth and cell division in green algae. Amer. Jour. Bot. 5: 271-279.

83. Breidenbach, A. W., Gunnerson, C. G. *et al*. 1967. Chlorinated hydrocarbon pesticides in major river basins. U.S. Public Health Rep. 82: 139-

84. British Columbia Research Council. 1967. The market for algicides. Mimeo. British Res. Council, Vancouver, B.C. 63 pp.

85. Britton, G., Fox, J. L. and Strickland, H. G. 1975. Removal of algae from Florida lakes by magnetic filtration. Appl. Microsc. 30: 905-908.

86. Brook, A. J. and Baker, A. L. 1972. Chlorination at power plants: impact on phytoplankton productivity. Science 176: 1414-1415.

87. Brouse, D. D. 1966. Copper sulphate air spray cures lake algae problem. Water & Pollution Control 104: 4, 25.

88. Brown, R. M. 1972. Algal viruses. Adv. in Virus Res. 17:243-277.

89. Brown, R. M., Smith, K. M. and Wayne, P. L. 1966. Replication cycle of the blue-green algal virus LPP-1. Nature 212: 729-730.

90. Browser, C. W. 1951. Rada for algae. The Reclamation Era 37: 247-248.

91. Browser, C. W. 1952. Progress report on field-scale demonstration with rosin amine D acetate to control algae (*Compsopogon* sp.) in irrigation drainage water. Res. Progr. Rep., 13th Western Weed Control Confer. 1952: 136, 137.

92. Brush, W. 1920. Treatment to counteract algae growths in large reservoirs. Jour. American Water Works Assoc. 7: 149-152.

93. Brush, W. 1920. Copper sulphate treatment to counteract algae growth in large reservoirs. Eng. Contract. 53: 432.

94. Burrows, R. E. and Combs, B. D. 1958. Lignasan as bactericide and algacide. Progr. Fish. Cultur. 20: 143.

95. Buscher, M. 1954. Untersuchungen uber den Aufwuchs in Wasserbecken und seine Bekampfung mit Kufersulphat. Schrift. Ver. f. Wasser.-Boden-und Lufthygiene. Berlin-Dahlem. No. 8.

96. Bussy, I. J. 1949. The growth and control of algae in open-air swimming pools. Comm. Zwembaden T. N. O. Rep. 1, Part 1. 78 pp.

96a. Bussy, I. J. 1952. Quaternary ammonium compounds as means of control of algae in open-air swimming pools. Res. Inst. Publ. Health Eng., T. N. O., Rep. No. 9: 1-39.

97. Bussy, I. J. 1969. Control of aquatic plant nuisances (especially algae) with some substituted phenylureas. Ver. Intern. Ver. Limnol. 17: 539-545.

98. Caird, J. M. 1904. Copper sulphate treatment for algae at Elmira, N.Y. Eng. News 52: 34.

99. Caird, J. M. 1905. Copper sulphate treatment for algae at Middletown, N.Y. Eng. News 53: 33-34.

100. Caird, J. M. 1935. Taste and odor control in public water supplies. Jour. New England Water Works Assoc. 49: 149-151.

101. Caird, J. M. 1945. Algae growth greatly reduced after stocking pond with fish. Water Works Eng. 98: 240.

102. Calvert, C. E. 1940. Treatment with copper sulphate, chlorine and ammonia. Jour. American Water Works Assoc. 32: 1155.

103. Calvert, C. E. 1941. The use of copper, chlorine & ammonia in plankton control. Jour. American Water Works Assoc. 33: 2108-2112.

104. Cameron, A. R. 1926. Control of algae growths in impounding reservoirs at Bucyrus. 6th Ann. Rep. Ohio Confer. Water Purification. pp. 30-32.

105. Campione, A. and Dhaliwal, A. S. 1975. Action of chloramphenicol and dimethylsulfoxide on the morphology of blue-green algae and plaque-forming ability of blue-green algal virus. Jour. Phycol. 11(Suppl.): 4. (Abstr.)

106. Cannon, R. E., Shane, M. S. and Whitaker, J. M. 1976. Interaction of *Plectonema boryanum* (Cyanophyceae) and LPP-cyanophages in continuous culture. Jour. Phycol. 12(4): 418-421.

107. Carlozzi, C. A. 1960. Farm pond weed control. N.Y. State Conserv. 14(5): 30-33.

108. Carpenter, E. J., Peck, B. B. and Anderson, S. J. 1972. Cooling water chlorination and productivity of entrained phytoplankton. Marine Biol. 16(1): 37-40.

109. Carpenter, L. V. 1928. Further instances of use of artificial turbidity for algae control. Eng. News Rec. 101: 852.

110. Carroll E. 1904. Treatment of a reservoir of the Butte Water Co. with copper sulphate. Eng. News Rec. 52: 141-143.

111. Casad, C. C. 1954. Watershed and reservoir control in the Pacific northwest. Algae and weed control. Jour. American Water Works Assoc. 46(8): 745-750.

112. Cason, C. E. 1930. Doctoring lakes and streams. Field & Stream 34(2): 58-64.

113. Catt, J. 1934. Copper sulphate in the elimination of coarse fish. Trans. Amer. Fish. Soc. 64: 276-279.

114. Cervenka, R., Stepanek, M. and Votarova, M. 1959. Limnological study of the reservoir Sedlice near Zeliv. VII. A contribution to the technique of selecting new algicide compounds. Inter. Chem. Tech., Prague, Soc. Technol., Fuel and Water 3(1): 247-290.

115. Chamberlain, W. J. 1948. Effects of algae on water supply. Univ. Queensland Papers, Dept. Chem. 1(29): 80 pp.

116. Chancellor, A. P. 1957. The control of aquatic weeds and algae. Rep. Agric. Res. Council Unit of Exper. Agronomy, Oxford.

117. Chancellor, A. P. 1958. The control of aquatic weeds and algae. History of Agric., Fisheries and Food, London. 20 pp.

118. Chapman, R. L. 1973. The presence of virus-like particles and concentrosomes in the M. B. Allen strain of *Porphyridium purpureum*. Jour. Phycol. 9(Suppl.): 16. (Abstr.)

118a. Chase, E. S. 1924. Copper sulphate treatment of Cape Pond, Rockport, Mass. Jour. New England Water Works Assoc. 38: 48.

118b. Clark, H. W. 1905. Investigations in regard to the use of copper and copper sulphate. Ann. Rep. Massachusetts State Bd. Health 11905.

119. Clark, W. F. 1954. Controlling weeds and algae in farm ponds. Cornell Exten. Bull. No. 910. 15 pp. New York College Agric., Ithaca, N.Y.

120. Cohen, C. 1927. Chlorination for algae control. Jour. American Water Works Assoc. 17: 444.

121. Cohen, C. 1928. Eliminating tastes and odors by algae in water. American City 38(4): 129, 130.

122. Cohen, C. 1933. Algae control in impounding reservoirs. Proc. 15th Ann. Texas Water and Sewage Works, Short School 1933.

123. Cohen, C. 1934. Algae control and references. Texas State Dept. Health Leaflet, 1934. 23 pp.

124. Cole, B. G. 1948. Taste and odor control at Shreveport. Jour. American Water Works Assoc. 40: 539-546.

125. Cook, S. T. 1926. A latent period in the action of copper on respiration. Jour. Gen. Physiol. 9: 651-675.

126. Cottam, C. 1954. Chemical controls in relation to wildlife. Presented before Pesticide Chemicals School, Clemson Agric. Coll., Clemson, S.C. 1954. pp. 1-11. (Mimeogr. by U.S. Fish & Wildlife Serv.)

127. Cox, C. R. 1936. A review of recent progress in the elimination of tastes and odors from water supplies. Jour. American Water Works Assoc. 28: 1855-1867.

128. Cox, C. R. 1948. Taste and odor control in water. Taste & Odor Control Jour. 14: 11.

129. Crance, J. H. 1963. The effects of copper sulphate on *Microcystis* and zooplankton in ponds. Progr. Fish Cultur. 25(4): 198-202.

130. Cushing, D. H. 1957. The effect of grazing in reducing the primary production. Rapp. P. V. Eeun. Cons. Inter. Explor. Mer 144: 149-154.

131. Daft, M. F. J., Begg, J. and Stewart, W. D. P. 1970. A virus of blue-green algae from fresh water habitats. New Phytol. (In Press, 1970).

132. Daft, M. F. J. and Stewart, W. D. P. 1971. Bacterial and viral pathogens of blue-green algae. British Jour. Phycol. 6(2): 268. (Abstr.)

133. Daft, M. F. J. and Stewart, W. D. P. 1971. Bacterial pathogens of fresh-water blue-green algae. New Phytol. 70(5): 319-329.

134. Darragh, J. L. and Stayner, R. D. 1954. Quaternary ammonium compounds from codecylbenzene. Algae control in industrial cooling systems. Ind. Eng. Chem. 46(2): 254-257.

135. Das, B. and Singh, P. K. 1977. Detoxication of the pesticide BHC by blue-green algae. Microbios Lett. 4(14): 99-102.

136. Davis, C. C. 1948. Studies of the effects of the industrial pollution in the lower Patapesco River area. 2. The effect of copper as pollution on plankton. Chesapeake Biol. Lab. Publ. No. 72: 3-12.

137. De Costa, J. D. and Laverty, G. L. 1964. Algal problems and their control at EBMUD (East Bay Municipal Utility District of Oakland, Calif.). Jour. American Water Works Assoc. 56: 1201-1203.

138. Derby, R. L. 1956. Chlorination of deep reservoirs for taste and odor control. Jour. American Water Works Assoc. 48: 75.

139. Deschiens, R. and Floch, H. 1964. Control of the action of selective molluscicides on the microfauna and microflora of fresh water. Bull. Soc. Path. Exotique 57: 292-299.

140. Distler, H. and Pommer, E. H. 1965. Control of algae growth in cooling systems with new microcides. Erdoel Kohle 18: 381-386.

141. Diven, J. M. 1924. Experience with $CuSO_4$ treatment of algae. Eng. Contr. 61: 380.

142. Domogalla, B. P. 1926. Treatment of algae and weeds in lakes at Madison, Wisconsin. Eng. News Rec. 97(24): 950-954.

143. Domogalla, B. P. 1935. Eleven years of chemical treatment of the Madison lakes: Its effects on fish and fish foods. Trans. American Fish. Soc. 65: 115-120.

144. Domogalla, B. P. 1941. Scientific studies and chemical treatment of the Madison lakes. A Symposium on Hydrobiology, Univer. Wisconsin Press, pp. 303-308.

145. Domogalla, B. P. 1956. Copper alkanolamine salts as algicides. U.S. Patent 2,734,028.

146. Doudoroff, P. and Katz, M. (Undated). The use of bromine for algae and slime control in the Los Angeles plant, Styrene Division. Dow Chemical Co., Midland, Michigan.

147. Eicher, G. 1947. Aniline dye in aquatic weed control. Progr. Fish Cultur. 1947: 39-42.

148. Eicher, G. 1948. Aniline dye in aquatic weed control. Jour. Wildlife Management 11: 193-197.

149. Eipper, A. W. and Brumsted, H. B. 1958. How to control weeds and algae in farm ponds. N.Y. Coll. Agric., Cornell Exten. Bull. 1014. 32 pp.

150. Eipper, A. W. and Forney, J. L. 1954. Control of filamentous algae in farm ponds. Farm Pond Res. Unit, Dept. Conserv., Cornell Univ.

151. Ellms, J. W. 1899. Water purification from Jackson's odors and tastes of surface waters. Odors and algicides. Tech. Quart. 10: 391.

152. Ellms, J. W. 1905. Behavior and uses of copper sulphate in the purification of hard and turbid waters. Jour. New England Water Works Assoc. 19: 496-503.

153. Ellms, J. W. 1928. Water Purification. McGraw-Hill Co. (Ed. 2).

154. Ely, H. M. 1922. Aerators and $CuSO_4$ for tastes and odors. Eng. News Rec. 89: 70, 71.

155. Emberley, G. 1912. The use of copper sulphate in purifying water supplies. Surveyor 42: 30, 31.

156. Emberley, G. 1917. Some experiences in the use of $CuSO_4$ in the destruction of algae. Analyst 42: 264-271.

157. Enright, J. T. 1969. Zooplankton grazing rates estimated under field conditions. Ecology 50: 1070-1075.

158. Enslow, E. H. 1933. Copper. (Editorial.) Water & Sewage Works 80: 110.

159. Farlow, W. G. 1876. Reports on peculiar conditions of the water supplied in the city of Boston. Rep. of the Cochituate Board, 1876.

160. Ferrax de Reyes, E. 1975. Effects of chlorinated insecticides on phytoplankton. Lagena 1973: 23-26.

161. Feygina, Z. S. 1945. The control of biological growths in waterworks. Gorod. Choz. Mosky 3: 26-28.

162. Fisher, A. 1956. The effect of copper sulphate on some microorganisms in fish ponds. Bamidgeh 8(2): 21-27.

163. Fitzgerald, G. P. 1957. The control of the growth of algae with CMU. Trans. Wisconsin Acad. Sci., Arts & Lettr. 46: 281-294.

164. Fitzgerald, G. P. 1959. Bacterial and algicidal properties of some algicides for swimming pools. Appl. Microbiol. 7: 205-211.

165. Fitzgerald, G. P. 1960. Loss of algicidal chemical in swimming pools. Appl. Microbiol. 8(5): 269-274.

166. Fitzgerald, G. P. 1961. Stripping effluents of nutrients by biological means. Algae and Metropolitan Wastes. Trans. 1960 Seminar, R. A. Taft Sanitary Eng. Center, USPHS, Tech. Rep. W-61-63.

167. Fitzgerald, G. P. 1962. Bioassay for algicidal chemicals in swimming pools. Water & Sewage Works 109: 361-363.

168. Fitzgerald, G. P. 1963. Field tests on the duration of algicides in swimming pools. Jour. Environ. Health 25: 319-325.

169. Fitzgerald, G. P. 1964. Factors in the testing and appreciation of algicides. Appl. Microbiol. 12: 247-253.

170. Fitzgerald, G. P. 1964a. Evaluation of potassium permanganate as an algicide for water cooling towers. Ind. Eng. Chem. Prod. Res. Develop. 3: 82-85.

171. Fitzgerald, G. P. 1964b. Laboratory evaluation of potassium permanganate as an algicide for water reservoirs. Jour. Southwest Water Works Assoc. 4(10): 16, 17.

172. Fitzgerald, G. P. 1965. Factors affecting the toxicity of copper to algae and fish. American Chem. Soc., Div. Water Waste Chem. Reprints 1963: 21-24.

173. Fitzgerald, G. P. 1966. Use of potassium permanganate for control of problem algae. Jour. American Water Works Assoc. 58(5): 609-614.

174. Fitzgerald, G. P. 1967. The algistatic properties of silver. Water & Sewage Works 114: 185-189.

175. Fitzgerald, G. P. 1968. Compatibility of swimming pool algicides and bactericides. Water & Sewage Works 115: 65-71.

176. Fitzgerald, G. P. 1971. Algicides. Univer. Wisconsin Water Resources Center, Lit. Rev. No. 2: 1-50.

177. Fitzgerald, G. P. 1975. Are chemicals used in algae control biodegradable? Water & Sewage Works 122: 82-85.

178. Fitzgerald, G. P. and DeVartanian, M. E. 1969. *Pseudomonas aeruginosa* for the evaluation of swimming pool chlorination and algicides. Appl. Microbiol. 17: 415-421.

179. Fitzgerald, G. P. and Faust, S. L. 1963. Factors affecting the algicidal and algistatic properties of copper. Appl. Microbiol. 11(4): 345-351.

180. Fitzgerald, G. P. and Faust, S. L. 1963a. Factors affecting the toxicity of copper to algae and fish. Amer. Jour. Bot. 50(6):

181. Fitzgerald, G. P. and Faust, S. L. 1963b. Bioassay for algicidal vs. algistatic chemicals. Water & Sewage Works 110(8): 296-298.

182. Fitzgerald, G. P. and Faust, S. L. 1965. Effects of bacteria on the solubility of copper algicides. Water & Sewage Works 112: 271-275.

183. Fitzgerald, G. P., Gerloff, G. C. and Skoog, F. 1952. Studies on chemicals with selective toxicity to blue-green algae. Sewage & Industr. Wastes 24(7): 888-896.

184. Fitzgerald, G. P. and Jackson, D. F. 1979. Comparative algicide evaluations using laboratory and field algae. Jour. Aquat. Plant Managem. 17: 66-71.

185. Fitzgerald, G. P. and Skoog, F. 1954. Control of blue-green algae blooms with 2,3-dichloronaphthoquinone. Sewage & Indust. Wastes 26(9): 1135-1140.

186. Fitzgerald, R. W. 1940. Latest development in taste and odor control. U.S. Public Health Abstr. 20(11): 50.

187. Fjerdinstad, E. 1956. A case of algal control in Denmark. Vattenhygien 2: 32-37.

188. Fleming, R. H. 1939. The control of phytoplankton populations by grazing. Jour. Couns. Explor. Mer 14: 1-

189. Flentje, M. E. 1945. Control and elimination of pest infestations in public water supplies. Jour. American Water Works Assoc. 37: 1194-1203.

190. Flentje, M. E. 1952. Control of algae and weeds in reservoirs. Jour. American Water Works Assoc. 44(8): 727-731.

191. Fleurent, E. and Levi, L. 1920. Presence of copper in the organism. Bull. Soc. Chem. 27: 440, 441.

192. Fogg, G. E. and Westlake, L. F. 1955. The importance of extracellular products of algae in freshwater. Proc. Intern. Assoc. Theor. and Appl. Limnol. 12: 219-232.

193. Foter, M. J., Palmer, C. M. and Maloney, T. E. 1953. Antialgal properties of various antibiotics. Antibiotics and Chemotherapy 3: 505-508.

194. French, D. K. 1922. Tastes and odors. Jour. American Water Works Assoc. 9: 899-905.

195. Fuller, G. W. 1909. Effects of hypochlorite on algae. Proc. American Water Works Assoc. 1909: 162-

196. Funk, W. H. and Gaufin, A. R. 1965. Control of taste- and odor-producing algae in Deer Creek Reservoir. Trans. Amer. Microsc. Soc. 84: 263-269.

197. Gallaher, W. W. 1940. Control of algae at Appleton, Wisconsin. Jour. American Water Works Assoc. 32(7): 1165-1175.

198. Garner, J. H. 1934. Sanitation and water purification. Rep. Progr. Appl. Chem. (Soc. Chem. Industry, London) 19: 733-771.

199. Garrett, J. E. 1965. Controlling microorganisms in cooling water systems. Nat'l Eng. 69(4): 6, 7.

200. Garrett, J. E. 1922. Use of copper sulphate at Hartford and effect on filter runs. Eng. News Rec. 89: 1124, 1125.

201. Garrett, J. E. 1922a. Application of copper sulphate to reservoirs. Canadian Eng. 43: 396, 397.

202. Gelfand, M. 1946. Algae control in water supplies. Power Plant Eng. 50: 63-65.

203. Gibbons, M. 1940. The use of Benoclor-3 in potable water supplies. Water & Sewage Works 87(5): 231.

204. Giliwicz, Z. M. 1975. Effect of zooplankton grazing on photosynthetic and composition of phytoplankton. Verh. Inter. Ver. Limnol. 19: 1490-1497.

205. Gilkinson, G. F. 1920. Novel application of $CuSO_4$ to basin walls for control of algae. Iowa Sec., American Water Works Assoc. 1920, Eng. Contr. 54: 468, 469.

206. Gilkinson, G. F. 1921. Application of $CuSO_4$ to basin walls to control algal growths. Jour. American Water Works Assoc. 8: 88-90.

207. Ginzburg, D., Padan, E. and Shilo, M. 1968. Effect of cyanophage infection on CO_2 photoassimilation in *Plectonema boryanum*. Jour. Virol. 2(7): 695-701.

208. Glaser, O. 1923. Copper, enzymes and fertilization. Biol. Bull. Marine Biol. Lab. 44: 79-103.

209. Goldstein, D. A., Bendet, I. J., *et al*. 1967. Some biological and physiological properties of blue-green algal virus LPP-1. Virology 32: 601-613.

210. Goodenough, A. H. 1905. Experiments upon the removal of microscopic organisms from ponds and reservoirs by the use of copper sulphate. Jour. New England Water Works Assoc. 19: 523-536.

211. Gopp, C. W. 1936. Plankton control in Norris reservoir. Jour. American Water Works Assoc. 28: 447-

212. Gorham, P. R. and Carmichael, W. W. 1979. Phytotoxins from blue-green algae. Pure & Appl. Chem. 52: 165-174.

213. Goryusgin, V. A. and Chaplinskaia, S. M. 1968. The discovery of viruses that lyse blue-green algae water blooms in the Dnieper water reservoirs, "Waterblooms." Ukranian Sci. Acad. 1968. pp. 171-174.

214. Goudey, R. F. 1936. A new method of copper sulphating reservoirs. Jour. American Water Works Assoc. 28(2): 163-179.

215. Goudey, R. F. 1938. Sunshine and algal control. Eng. News Rec. 120(16): 581, 582.

216. Goudey, R. F. 1944. Algicides. Water Works Eng. 97(25): 1461, 1462.

217. Goudey, R. F. 1946. Chemical weed control. American Water Works Assoc. 38: 186-202.

218. Goulding, K. H. 1971. A preliminary investigation of a potential new algicide. Proc. 6th British Insecticide and Fungicide Confer. pp. 66-124.

219. Gowanloch, J. N. and Rajkov, A. D. 1947. Water hyancinth program. State of Louisiana, 2nd Biennial Rep.: Wildlife and Fish. 1946-1947: 66-124.

220. Gratteau, J. G. 1970. Potential algicides for the control of algae. Water & Sewage Works 1970. Ref. No. 117: R24-R61.

221. Green, B. R. 1946. The algicidal effects of 2, 4-dichlorophenoxy-acid and some of its derivatives. M.A. Thesis, Ohio State Univ.

222. Greenwald, M. 1954. List of references on control of aquatic plants including algae. Res. Div. Chipman Chem. Co., Bound Brook, N.J.

223. Greenwald, M. 1956. List of references on control of aquatic plants including algae. Res. Div., Chipman Chem. Co., Bound Brook, N.J.

224. Griffiths, B. M. 1938. Early references to waterbloom in British lakes. Proc. Linn. Soc. London, Bot. 151: 12-19.

225. Guseva, K. A. 1952. Waterbloom, its causes, prediction, and control. Trudy Vses Girodbiol. Obscgchestva Akad. Nauk SSSR 4: 3-92.

226. Haine, W. 1918. Control of microscopic organisms in water supplies. Jour. New England Water Works Assoc. 32: 18-20.

227. Hale, F. E. 1925. The use of copper sulphate in the control of microscopic organisms. Phelps Dodge Corp., New York. 44 pp.

228. Hale, F. E. 1926. New York's experiment with $CuSO_4$. Public Water 57: 221-223.

229. Hale, F. E. 1926a. Algae treatment of reservoirs. Jour. American Water Works Assoc. 16: 765-768.

230. Hale, F. E. 1927. Algae treatment of reservoirs. Water Works Eng. & Contr. 66: 83, 84.

231. Hale, F. E. 1943. Control of algae (in water supplies). Water & Sewage Works Ref. & Data Sec. 90: R139, R140.

232. Hale, F. E. 1946. Control of algae. Water & Sewage Works. 93: R173, R174.

233. Hale, F. E. 1947. Water treatment in Maine. Jour. American Water Works Assoc. 39: 77, 78.

234. Hale, F. E. 1949. Control of algae. Water & Sewage Works 96, Ref. & Data Sec.: R95, R96.

235. Hale, F. E. 1950. The use of copper sulphate in control of microscopic organisms. Phelps Dodge Corp., New York. pp. 1-43.

236. Hale, F. E. and Muer, H. F. 1926. Copper in water distribution system following watershed treatment. Jour. American Water Works Assoc. 15: 650-653.

237. Hall, G. A. 1936. The algae problems at Norwalk. 15th Ann. Rep. Ohio Confer. on Water Purification, Cleveland. 58 pp.

238. Hall, T. F. and Hess, A. D. 1947. Studies on the use of 2, 4-L for the control of plants in a malaria control program. Jour. Nat. Malaria Soc. 6(2): 99-116.

239. Handley, D. E. 1949. A summary of four years of chemical control of aquatic vegetation at Buckeye Lake, Ohio. State of Ohio Div. Wildlife, Dept. Nat. Res., Bull. 244. (Mimeogr.)

240. Haney, J. F. 1971. An *in situ* method for the management of zooplankton grazing rates. Limnol. & Oceanogr. 15: 839-928.

241. Haney, J. F. 1973. An *in situ* examination of the grazing activities of natural zooplankton communities. Arch. d. Hydrobiol. 72: 87-132.

242. Hardy, E. 1963. The control of aquatic plants in fish waters. I. Salmon & Trout Mag. 167: 64-69. II, Ibid., Ibid.: 121-128.

243. Hargrave, B. T. and Green, G. H. 1970. Effects of copepod grazing on two natural phytoplankton populations. Jour. Fish. Res. Bd. Canada 27: 1395-1403.

244. Harlock, C. R. and Dowlin, M. P. 1953. Chlorine and chlorine dioxide for the control of algae odor. Water & Sewage Works 100: 74, 75.

245. Harold, C. H. H. 1937. Present day aspects of the purification of London water supply. Water & Water Eng. 39: 388.

246. Harris, B. B. and Silvey, J. K. G. 1948. Algae control in fresh water or municipal reservoirs of the southwest, Southwest Water Works Jour. 14: 11-14.

247. Harris, D. O. 1970. An autoinhibitory substance produced by *Platydorina caudata* Kofoid. Plant Physiol. 45: 210-214.

248. Harris, D. O. 1971. A model system for the study of growth inhibitors. Arch. f. Protistenk. 113: 230-234.

249. Harris, D. O. 1971a. Growth inhibitors produced by the green algae (Volvocaceae). Arch. Mikrobiol. 76: 47-50.

250. Harris, D. O. and Parekh, M. C. 1974. Further observations on an algicide produced by *Pandorina morum*, a colonial green flagellate. Microbios 9: 259-265.

251. Hartman, B. J. 1961. Licking the algae problem. Water Works Eng. 114: 435, 476, 477.

252. Hartung, H. O. and Lischer, V. C. 1942. Carbon blackout as a means of preventing algae growth. Taste & Odor Control Jour. 8(8): 1-3.

253. Harvey, H. W., Cooper, L. N. H., Lebour, N. V., and Russell, F. S. 1935. Plankton production and its control. Jour. Mar. Biol. Assoc., United Kingdom 20: 407-441.

254. Hasler, A. D. 1947. The case against spraying $CuSO_4$ on lakes. Trans. Wisconsin Acad. Sci., Arts & Lettr. 1947.

255. Hasler, A. D. 1947a. Eutrophication of lakes by domestic drainage. Ecology 28(4): 385-395.

256. Hasler, A. D. 1949. Antibiotic aspects of copper treatment of lakes. Trans. Wisconsin Acad. Sci., Arts & Lettr. 39: 97-103.

257. Hassler, J. W. and Faye, M. 1945. Influence of various chemicals on palatability of drinking water. Taste & Odor Control Jour. 11: 3.

258. Hassler, W. W. 1941. The history of taste and odor control. Jour. American Water Works Assoc. 33: 2124-2152.

259. Hawkins, A. F. 1972. Control of algae. Outlook on Agric. 7(1): 21-26.

260. Hawxby, K., Tubea, B., et al. 1977. Effects of various classes of herbicides on 4 species of algae. Pesticide Biochem. Physiol. 7(3): 203-209.

261. Hazzard, A. S. 1962. Causes, effects and control of aquatic growth. Jour. Water Pollu. Control Fed. 34: 289-290.

262. Hercules Powder Co. 1954. Delrad algicide for control of algae in lakes, ponds, and irrigation systems. Hercules Powder Co., Chemical Div., Naval Store Dept., Wilmington, Delaware, Bulletin.

263. Hercules Powder Co. 1955. Delrad toxicology Report. Booklet. 9 pp.

264. Herman, E. F. and Anderson, W. 1947. Control of algal growths in hatching ponds and raceways. Progr. Fish Cultur. 9(4): 211-212.

265. Hirsch, A. A. 1942. Toxic effects of sodium pentachlorophenate and other chemicals on water hyacinth. Bot. Gaz. 103: 620-621.

266. Hodgson, J. M. 1952. Controlling algae with rosin amine D acetate. Res. Progr. Rep., 13th Western Weed Control Confer. p. 136.

267. Hoffman, D. A. and Olive, J. R. 1961. The effects of rotenone and toxaphane upon plankton of two Colorado reservoirs. Limnol. & Oceanogr. 6(2): 219-222.

268. Hoffman, L. R. and Stanker, L. H. 1975. Virus-like particles in the green alga Cylindrocapsa. Jour. Phycol. 11(Suppl.): 7. (Abstr.)

269. Hollister, T. A. and Walsh, G. E. 1973. Differential response of marine phytoplankton to herbicides: oxygen evolution. Bull. Environ. Contam. & Toxicol. 9(5): 291-295.

270. Holtje, R. H. 1939. Some trouble-makers in reservoirs. Jour. American Water Works Assoc. 31(3): 550-557.

271. Hood, J. W. 1954. Copper sulphate for root and fungus control in sanitary sewers and storm drains. Phelps Dodge Refining Co. Booklet. 24 pp.

272. House, G. O. and Huff, N. L. 1916. Copper sulphate treatment of St. Paul, Minnesota water supply. Jour. American Water Works Assoc. 3: 581-621.

273. Howard, N. J. 1947. Taste and odor treatment. Water Works Eng. 93(8): 420-423.

274. Howard, N. J. and Berry, A. E. 1933. Algae nuisances in surface waters. Canadian Publ. Health Jour. 24(7): 377-384.

275. Hueck, H. J. and Adema, D. M. M. 1967. Some problems in the testing of materials with algae. Central Lab. TND, DELFT (Netherlands) 2(2): 141-152.

276. Huff, N. L. 1916. Response of microorganisms to copper sulphate treatment. Minn. Bot. Stud. 4: 407-425.

277. Huff, N. L. 1922. $CuSO_4$ treatment for preventing algae growths in lakes and reservoirs. Municip. Surv. & Eng. Soc. Canada. Eng. 43: 298-301.

278. Huff, N. L. 1922a. Copper sulphate treatment for preventing algae growths in lakes and reservoirs. Water Works News 1922: 65-72.

279. Huff, N. L. 1926. Algae in water supplies. Jour. American Water Works Assoc. 15: 498-504.

280. Husband, J. W. 1933. Algal growths and water supply. Water & Eng. 35: 765-780.

281. Imbeaux, E. 1937. Sur la destruction du plancton dans les eaux potables. Rev. d'Hygiene, Paris 59: 664-666.

282. Inertol Co., Inc. 1955. Exalgae, effective algicide. Company Folder 776-A. 4 pp.

283. Ingram, W. M. 1953. Handbook of selected biological references on water pollution control, sewage treatment, water treatment. Publ. Health Bibliography Ser. 8. 66 pp.

284. Ingram, W. M. and Prescott, G. W. 1954. Toxic fresh-water algae. American Mid. Nat. 52(1): 75-87.

285. Ingram, W. M. and Tarzwell, C. M. 1954. Selected bibliography of publications relating to undesirable effects upon aquatic life by algicides, insecticides, weedicides. Publ. Health Bibliography Ser. 13: 1-28.

286. Insalata, N. F. 1953. Balking algae in beverage water. Food Eng. 24(12): 72-74.

287. Isaac, P. C. and Lodge, M. 1958. Algae and sewage treatment. New Biol. 25: 85-97.

288. Ives, K. J. 1957. Algae and water supplies. III. Control of algae in reservoirs. Water & Water Eng. 61: 387-389.

289. Jackson, D. and Sladecek, V. 1970. Algal virus-eutrophication control potentials. Yale Scientif. 44: 16-21.

290. Jackson, D. D. 1905. Purification of water by copper sulphate. Municip. Eng. 29: 245, 246.

291. Jackson, D. D. 1905a. Discussion of copper sulphate. Jour. New England Water Works Assoc. 19: 563-568.

292. Jaero, J. W. 1928. Chemicals destroy lake weeds: How Madison, Wisconsin has solved the problem of ridding nearby lakes of obnoxious weed growths and algae. Sci. Amer. 138: 532, 533.

293. Jakob, N. and Nisbet, M. 1955. Effect of certain quaternary ammonium derivatives on some fresh-water fish and algae. Verh. Intern. Ver. Limnol. 12: 726-

293a. Janik, J. J., W. D. Taylor and J. W. Barko. 1980. A compilation of common algal control and management techniques. Technical Report E-80-1. Waterways Experiment Station, Corps of Engineers, Vicksburg, Mississippi. 53 pp.

294. Jansen, L. L., Gentner, W. A. and Hilton, J. L. 1958. A new method for evaluating potential algicides and determination of the algicidal properties of several substitute-urea and s-triazine compounds. Weeds 6(4): 390-398.

295. Johnson, E. E. 1930. Algae and their control. Proc. 5th Ann. Meeting Kentucky-Tennessee Sec. American Water Works Assoc., Lexington. pp. 70-79.

296. Johnson, L. D. 1955. Control of Ulothrix zonata in circular ponds. Progr. Fish. Cultur. 17: 126-128.

297. Jordan, L. S., et al. 1962. Chemical control of filamentous green algae. Hilgardia 32: 433-441.

298. Jørgensen, E. G. 1956. Growth inhibiting substances formed by algae. Physiol. Plant. 9: 712-726.

299. Jung, W. 1954. Algal growth and control in open-air baths. Arch. Radewaesens 6(5): 197.

300. Kar, S. and Singh, P. K. 1978. Effect of pH, light intensity and population on the toxicity of the pesticide carbofuran to the blue-green alga *Nostoc muscorum*. Bull. Environ. Control Toxicol. 20(5): 707-714.

301. Keating, K. I. 1976. Interference by blue-green algae with nutrient recovery in water quality control scheme: Management implications. In: Biological control of water pollution. J. Tourbier and Robert W. Pierson, Jr., Eds. Univ. Pa. Press.

302. Keating, K. I. 1978. Blue-green algal inhibition of diatom growth: Transition from mesotrophic to eutrophic community structure. Science 199: 971-973.

303. Kellerman, K. F. 1912. The rational use of disinfectants and algicides in municipal water supplies. 8th Intern. Congr. Appl. Chem. 26:241-245.

304. Kellerman, K. F. and Beckwith,, T. D. 1906. The effect of copper upon water bacteria. U.S.D.A. Agric. Bur. Plant Indust. 100(7): 1-19.

305. Kemp, H. T., Fuller, R. G. and Davidson, R. S. 1960. Potassium permanganate as algicide. Jour. American Water Works Assoc. 58(2): 255-

306. Khoboy'ev, V. G., Kapkov, V. I. *et al*. 1975. Toxicity of copper containing compounds for algae. Gidrobiol. Zeit. 11(5): 49-55.

307. Kinnicut, L. P. 1905. Purification of water by copper sulphate. Rev. American Chem. Res. 11: 675-

308. Koch, D. 1964. Control of algae in the "Hochenfreibad Killesberg", Stuttgart. Arch. Badeswesens 5: 37-

309. Kocurova, E. 1966. The application of the algicide Ca-350 in the Lubi Reservoir near Trebic. Hydrobiologia 28(2): 223-240.

310. Kott, Y. and Edlis, J. 1969. Effect of halogen on algae. 1. *Chlorella sorokiniana*. Mekdroth Water Co., Water Res. 3: 251-256.

311. Kraemer, H. 1904. The copper treatment of water. American Jour. Pharm. 76: 574-579.

312. Kraus, M. P. 1973. Lysogeny in the blue-green algae. Jour. Phycol. 9(Suppl.): 16. (Abstr.)

313. Krohnke, B. 1893. Suggestions for the improvement and sterilization of surface water by chemical methods, with special reference to the Elbe water at Hamburg. Jour. f. Gasbeleuchtung u. Wasserrersorgung 36: 513-

314. Kumar, H. D. 1965. Effect of certain toxic chemical and mutagens on the growth of the blue-green alga *Anacystis nidulans*. Canadian Jour. Bot. 43: 1523-1532.

315. Kuran, O. and Angell, H. H. 1953. Rout reservoir algae. American City 68: 90.

316. Lackey, J. B., Lackey, E. W. and Morgan, G. B. 1964. Iodine as an algicide in swimming pools. Eng. Progr. Univ. Florida 18(3): 1-

317. Lacroix, J. D. 1950. Effects of butyl ester of 2, 4-D on some algae. Indiana Acad. Sci. Proc. 59: 44, 45 (Abstr.)

318. Lawrence, J. M. 1954. Control of a branched alga, *Pithophora*, in farm fish ponds. Progr. Fish Cultur. 16(2): 83-87.

319. Lawrence, J. M. and Thomaston, W. W. 1956. Results of tests on the use of Delrad to control filamentous algae in fish ponds and its effect on fish and fish-food production. (Unpublished Manuscript in 1956).

320. Lawton, G. W. 1961. The Madison lakes before and after diversion. In: Algae and Metropolitan Wastes Conference, R. A. Taft Sanitary Eng. Center, Tech. Rep. W61-3.

321. Le Cosquino de Bussy, I. J. 1969. Control of aquatic plant nuisances (especially algae) with some substitued phenylureas. Verh. Intern. Ver. Limnol. 17: 539-545.

322. Lefevre, M. and Jakob, H. 1949. Sur quelques properietes des substances actives tirees des culture d' algues d'eau douce. Compt. Rend. Acad. Sci. Paris 229: 234-236.

323. Leibee, H. C. and Smith, R. I. 1953. Control of algae-- a means of prolonging the life of lakes. Waste Eng. 24: 620, 621.

324. Lendall, H. N. 1946. A comprehensive survey of the taste and odor problem. Taste & Odor Control Jour. 12(10): 1-8.

325. Levardsen, N. O. 1953. Experiments with nigrosine dye in aquatic plant control. Progr. Fish Cultur. 15(3): 109-113.

326. Lewis, D. E. 1930. Copper sulphate clears algae trouble at Winslow. Municip. Sanita. 1:442.

327. Lindsay, J. 1912. The elimination of algae in locks and ponds. Trans. Edinburgh Field Nat. Microsc. Soc. 1911-1912: 422-431.

328. Lodge, M. and Isaac, P. C. G. 1958. Control of algae in a reservoir. Jour. Inst. Water Eng. 12: 198-

329. Lovejoy, W. H. 1928. Algae control by creating turbidity at Louisville. Eng. News Rec. 101: 505-507.

330. Luftig, R. and Haselkorn, R. 1967. Morphology of a virus of blue-green algae and properties of its deoxyribonucleic acid. Jour. Virol. 1: 344-361.

331. Lund, J. W. G. 1955. The ecology of algae and waterworks practice. Proc. Soc. for Water Treatment and Examination 4: 83-109.

332. Mackenthun, K. M. 1951. Water weed and algae control in Wisconsin. 13th Midwest Wildlife Confer., Minneapolis. 7 pp.

333. Mackenthun, K. M. 1952. Selected review of the literature on toxic materials affecting biological life in streams and sewage treatment processes. Wisconsin Comm. on Water Pollution, Madison. 45 pp. (Mimeogr.)

334. Mackenthun, K. M. 1952a. Cleaner lakes can be a reality. Wisconsin Conserv. Bull. 17(1): 1-4.

335. Mackenthun, K. M. 1954. Aquatic nuisance control progress report. Wisconsin Comm. on Water Pollution, Madison. 5 pp.

336. Mackenthun, K. M. 1958. The chemical control of aquatic nuisances. Wisconsin Comm. on Water Pollution, Madison. 64 pp.

337. Mackenthun, K. M. 1960. What you should know about algae control. Public Works 91(9): 114-116, 160, 162.

338. Mackenthun, K. M. 1961. The practical use of present algicides and modern trends toward new ones. In: Algae and Metropolitan Wastes, pp. 148-154. U.S. Publ. Health. (Trans. Seminar, Cincinnati, Ohio).

339. Mackenthun, K. M. 1962. A review of algae, lake weeds and nutrients. Jour. Water Pollut. Control Fed. 34(10): 1077-1085.

340. Mackenthun, K. M. 1969. The practice of water pollution biology. Water Pollut. Control Fed. 281 pp.

341. Mackenthun, K. M. and Cooley, H. L. 1952. The biological effect of copper sulphate treatment of lake ecology. Trans. Wisconsin Acad. Sci., Arts & Lettr. 41: 177-187.

342. Mackenthun, K. M. and Ingram, W. M. 1967. Biological associated problems in freshwater environments. Their classification, investigation and control. Water Pollut. Control Fed., Cincinnati, Ohio. 285 pp.

343. Mackenthun, K. M. and Keup, L. E. 1970. Biological problems encountered in water supplies. Jour. American Water Works Assoc. 62(8): 520-526.

344. Mahlie, W. S. 1923. Algae control in Texas. Jour. American Water Works Assoc. 10: 998-1010.

345. Majid, F. Z. and Nahar, L. 1970. Control of phytoplanktons in polluted ponds in East Pakistan, using copper sulphate after Phelps Dodge Refining Corporation, N.Y. Sci. Res. East Reg. Lab., Pakistan 7(1): 56-60.

346. Malherbe, H. H. and Strickland-Cholmely, M. 1967. Survival of viruses by the water route. (Berg, Ed). Interscience Press, N.Y. pp. 449-470.

347. Maloney, T. E. 1958. Control of algae with chlorophenyl dimethyl urea. Jour. American Water Works Assoc. 62(8): 520-526.

348. Mallory, F. B. 1927. Poisonous effects of copper. Jour. New England Water Works Assoc. 41:

349. Manguin, L. B. 1928. Algae control in uncovered distribution reservoir by chlorinating. Municip. News & Water Works 75: 103, 104.

350. Manguin, L. B. 1929. Algae control by chlorination at Kansas City. Jour. American Water Works Assoc. 41(1): 27-30.

351. Manguin, L. B. 1929a. The identification and control of algae. Municip. News & Water Works 76: 199-201. (Title varies).

352. Manguin, L. B. 1929b. Identification and control of algae types in water supplies. Water Works Eng. 82: 607, 608.

353. Manguin, L. B. 1929c. Algae control at Kansas City, Kansas. Jour. American Water Works Assoc. 21(1): 44-49.

354. Marquis, J. K. 1932. Copper sulphate as an algicide. Jour. American Water Works Assoc. 24(5): 728-732.

355. Marsh, M. C. et al. 1908. The treatment of fish-cultural waters for the removal of algae. Bull. U.S. Bur. Fish. 28: 871-890.

356. Marvin, K. T. et al. 1961. Effects of copper ore on the ecology of a lagoon. U.S. Fish & Wildlife Serv., Fish. Bull. 61(184): i-iv + 153-160.

357. Marx, A. J. 1951. Pre-treatment basin for algae removal. Taste & Odor Control Jour. 17(6): 1-8.

358. Matheson, D. H. 1953. Algae control in small water plants. Jour. American Water Works Assoc. 45: 1238-1244.

359. Matheson, D. H. 1953a. Algae control in small waterworks. Municip. Util. 91: 54.

360. Matheson, D. H. 1956. Taste and odor control in small water plants. Water & Sewage Works, (Ref. & Data Sec.) 103: R192-R195.

361. May, V. 1972. Blue-green algal blooms at Braidwood, New South Wales (Australia). New South Wales Dept. Agric. Sci. Bull. 82. 45 pp.

362. May, V. 1974. Suppression of blue-green algal blooms in Braidwood Lagoon with alum. Jour. Australian Inst: Agric., Sci. 40: 54-

363. May, V. and Baker, H. 1978. Reduction of toxic algae in farm dams by ferric alum. New South Wales Dept. Agric., Tech. Bull. 19: 1-16.

364. McGeorge, W. T. 1946. Experiments with Benoclor. Rep. to Salt River Valley Water User's Assoc., Univ. Arizona Coll. Agric. Exper. Station.

365. McIntyre, F. J. 1949. Algae control--swimming pools. Water & Sewage Works 96: 196.

366. McKee, G. D., Paris, L. P., et al. 1970. Sediment-water nutrient relationship. Part II. Water & Sewage Works 117: 246-249.

367. McMullin, H. L., et al. 1949. Control of algae and plant growth in water storage reservoirs. Water Service & Sanitation, American Railway Eng. Assoc. Bull. 483. pp. 155-157.

368. Medbury, H. C. 1946. Algae control in reservoirs of San Francisco system. Water Works Eng. 99: 14-16.

369. Meerovich, M. and Moisseyeva, L. 1928. Acute copper sulphate poisoning. Deutsch. Ges. Bericht Med. 11: 189-192.

370. Monie, W. D. 1941. Algae control. Jour. American Water Works Assoc. 33(4): 705-720.

371. Monie, W. D. 1944. A copper sulphate test for algal control. Taste & Odor Control Jour. 10(8):

372. Monie, W. D. 1946. Pre-determining effective dosage of copper sulphate in algae control. Water & Sewage Works 93: 173-176.

373. Monie, W. D. 1947. Pre-determing effective dosage of copper sulphate in algae control. Water & Sewage Works 94: 118-120.

374. Monie, W. D. 1951. Algal control. Taste & Odor Control Jour. 17: 1-7.

375. Monie, W. D. 1952. Pre-determining effective dosage of copper sulphate in algae control. Water & Sewage Works 99 (Ref. & Data Sec.): R96-R98.

376. Monie, W. D. 1956. Algae control with copper sulphate. Water & Sewage Works 103(9): 392-397.

377. Montagne, M. 1856. Sur deux algues nees pendant les experiences de M. Boussingault, relatives a l'action du saltpetre sur la vegetation. Compt. Rend. Acad. Sci. 42: 756-764. (Historical interest).

378. Montemartin, L. 1920. The stimulating action of copper sulphate on plants. Rev. Patol. Veg. 10: 36-40.

379. Moore, G. T. (1902) 1903. The contamination of public water supplies by algae. Yearbook Dept. Agric. 1902: 175-186.

380. Moore, G. T. 1904. A new method for the purification of water supplies. Amer. Jour. Pharm. 76(12): 553-564.

381. Moore, G. T., Jackson, D. D., *et al*. 1905. A symposium on the use of copper sulphate and metallic copper for the removal of organisms and bacteria from drinking water. Jour. New England Water Works Assoc. 19(4): 474-582.

382. Moore, G. T. and Kellerman, K. F. 1904. A method of destroying or preventing the growth of algae and certain pathogenic bacteria in water supplies. U.S. Dept. Agric., Bur. Plant Indust. Bull. 64: 1-44.

383. Moore, G. T. and Kellerman, K. F. 1905. Copper as an algicide and disinfectant in water supplies, U.S. Dept. Agric., Bur. Plant Indust. Bull. 76. 55 pp.

384. Moran, W. T. and Shaw, J. M. 1948. A new killer for water weeds. Reclamation Area 34: 81-84.

385. Moravcova, V. 1965. Survey of literature on the application of algicides. Ustav Ved. Tech. Inform, Prague, No. 2.

386. Moravcova, V. 1967. Biological investigations of an infiltration area and experiments with some algicides. Hydrobiologia 29(3/4): 505-646.

387. Morgan, O. D. 1959. Chemical control of algae and other nuisance growths on greenhouse benches, pots and potting soil. Plant Des. Rep. 43: 660-663.

388. Moss, D. 1956. Algae control investigations. Alabama Dept. Conserv, Fish. Sec. 15 pp. (Mimeogr.)

389. Moudry, Z. V. and Moudry, M. K. 1960. Liquid oligodynamic compositions useful as algicides. U.S. Patent 2,902,400.

390. Moyle, J. B. 1949. The use of copper sulphate for algal control and its biological implications. In: Limnological Aspects of Water Supply & Waste Disposal, AAAS Publ. 1949. pp. 79-87.

391. Moyle, J. B. and Wilson, J. N. 1946. Report on the use of copper sulphate for controlling blue-green algae in Hall Lake (2-83) and connected water supply lakes in Martin County. Minnesota Dept. Conserv. & Health, 1946.

392. Mulligan, F. 1969. Management of aquatic vascular plants and algae. Cornell Univ. Dept. Bot. - Eutrophication: causes, consequences, correctives. pp. 464-482.

393. Nagy, D. E. 1965. 1-alkylphenyl-2, 2-di-lower alkyl-4, 6-diiminohexahydro-s triazine. U.S. Patent 3,168,519.

394. Naman, E. O. 1970. Algicidal evaluation and environmental study of mat-producing blue-green algae. Bureau of Reclamation, Denver, Colorado, Office of Chief Engineer. 50 pp.

395. Nesin, B. J. and Derby, R. L. 1954. Methods of controlling aquatic growths in reservoirs. Jour. American Water Works Assoc. 46: 1141-

396. Nichols, M. S., Henkel, T. and McNaul, D. (1946) 1947. Copper in lake muds from lakes in the Madison area. Trans. Wisconsin Acad. Sci., Arts & Lettr. 38: 333-350.

397. O'brien, G. 1943. Taste and odor control by reservoir chlorine blanket. Water Works Eng. 96(18): 996-999.

398. O'brien, G. 1966. Dichlone as a control for algae and submersed aquatic weeds. U.S. Rubber Co., Bethany Information Sheet No. 82. 5 pp.

399. O'Donnell, J. 1943. Control of *Hydrodictyon reticulatum* in small ponds Trans. Amer. Fish. Soc. 73: 59-62.

400. Olson, T. A. 1949. History of toxic plankton and associated phenomena. Sewage Works Eng. 20(2): 71-

401. Opie, V. 1940. Blackout of algae with activiated carbon. Taste & Odor Control Jour. 6(11): 1, 2.

402. Oswald, W. J. and Golueke, C. G. 1968. Harvesting and processing of waste-grown microalgae. In: Algae, Man and Environment. pp. 371-389.

403. Padan, E., Ginzburg, D. and Shilo, M. 1970. The reproductive cycle of cyanophage LPP-1G and its dependence on photosynthetic and respiratory systems. Virology 40: 514-521.

404. Padan, E. and Shilo, M. 1969. Distribution of cyanophages in natural habitats. Verh. Inter. Ver. Limnol. 17: 514-521.

405. Padan, E. and Shilo, M. 1969a. Spread of viruses attacking blue-green algae in freshwater ponds, and their interaction with *Plectonema boryanum*. Bamidgeh 20: 77-87.

406. Padan, E. and Shilo, M. 1973. Cyanophages-viruses attacking blue-green algae. Bacter. Rev. 37: 343-370.

407. Padan, E., Shilo, M. and Kislev, N. 1967. Isolation of cyanophages from freshwater ponds and their interaction with Plectonema boryanum. Virology 32: 234-246.

408. Paine, B. B. 1963. How to keep algae out of your pool. Flower Grower 40: 42-45.

409. Palmer, C. M. 1956. Evaluation of new algicides for water supply purposes. Jour. American Water Works Assoc. 48(9): 1133-1137.

410. Palmer, C. M. 1956a. New algicides. Jour. American Water Works Assoc. 48(10): 1234-

411. Palmer, C. M. 1956b. Toxicity of six chemical compounds to thirty cultures of algae. Water & Sewage Works 1956:

412. Palmer, C. M. 1956c. Control of algae in swimming pools. Jour. American Med. Assoc. 162: 938-

413. Palmer, C. M. 1957. Evaluation of new algicides for water supply purposes. taste & Odor Control Jour. 23(1): 1-4.

414. Palmer, C. M. 1959. Algae in water supplies. Publ. Health Ser. No. 657. R. A. Taft Sanitary Eng. Center, Cincinnati, Ohio.

415. Palmer, C. M. 1961. Algae and other interference organisms in water supplies of California. Jour. American Water Works Assoc. 53(10): 1297-1312.

416. Palmer, C. M. 1964. Algae in water supplies of the United States. In: Algae and Man, Chap. 12. Plenium Press, New York.

417. Palmer, C. M. 1967. Biological aspects of water supply and treatment in Virginia with particular reference to algae. Virginia Jour. Sci. 18(1): 6-12.

418. Palmer, C. M. 1967a. Algae and associated organisms in West Virginia waters: problems and control measures. Castanea 32: 123-133.

419. Palmer, C. M. and Ingram, M. 1955. Suggested classification of algae and protozoa in sanitary science. Sewage & Indust. Wastes 27: 1183-1188.

420. Palmer, C. M. and Maloney, T. E. 1955. Preliminary screening for potential algicides. Ohio Jour. Sci. 55(1): 1-8.

421. Palmer, C. M. and Poston, W. 1956. Algae and other interference organisms in Indiana water supplies. Jour. American Water Works Assoc. 48(10): 1335-1346.

422. Parker, B. C. 1956. Control of fresh-water algae. Yale Conserv. Stud. 5: 35-40.

423. Pearson, B. R. and Norris, R. E. 1974. Intranuclear virus-like particles in the marine alga *Platymonas* sp. (Chlorophyta, Prasinophyceae). Phycologia 13(1): 5-9.

424. Peelen, R. 1969. Possibilities to prevent blue-algal growth in the Delta region of the Netherlands. Verh. Intern. Ver. Limnol. 17: 763-766.

425. Perkins, R. N. 1946. Control of algae by Perkins C-34: Pool Problems Bull. No. 25: 1-49.

426. Perkins, R. N. 1946a. Control of algae by Perkins XY-10. Pool Problems Bull. No 3 1/2: 1-13.

427. Perkins, R. N. 1946b. Control of algae by Perkins CM-21. Refinite Corp. Bull. No. 26: 1-24.

428. Perlman, D. 1964. Antibiotic inhibition of algal growth. In: Antimicrobial Agents and Chemotherapy. pp. 114, 115.

429. Peterka, H. J. and Held, J. W. 1972. Cause and control of algal blooms in Spiritwood Lake, North Dakota. North Dakota Univ. Water Res. Inst., Project Tech. Bull. B-001-NDAJ 1972. 18 pp.

430. Phelps, R. A. and Schlichting, H. E. 1968. The use of Warburg apparatus to test algicidal compounds. Adv. Front. Plant Sci. 19: 181-194.

431. Pickett-Heaps, J. D. 1972. A possible virus infection in the green alga *Oedogonium*. Jour. Phycol. 8: 44-47.

432. Piennar, R. N. 1976. Virus-like particles in three species of phytoplankton from San Juan Island, Washington. Phycologia 15(2): 185-190.

433. Pierce, M. E. 1958. The effect of the weedicide Kuron upon the flora and fauna of two experimental areas of Long Pond, Dutchess County, N.Y. Proc. Northeast. Weed Control Confer. 12: 338-343.

434. Pierce, M. E. 1959. Further study of the effect of the weedicide Kuron upon the flora and fauna of Long Pond, Dutchess County, New York. Proc. Northeast. Weed Control Confer. 13: 310-314.

435. Pierce, M. E. 1960. Progress report of the effect of Kuron upon the biota of Long Pond, Dutchess County, New York. Proc. Northeast. Weed Control Confer. 14: 472-475.

436. Pierce, M. E. 1960a. A study of the effect of the weed killer, 2,4-D granular on three experimental plots of Long Pond, Dutchess County, N.Y. Proc. Northeast. Weed Control Confer. 14: 483-487.

437. Pierce, M. E. 1961. A study of the effect of the weed-killer, 2, 4-D aqua granular on six experimental plots of Long Lake, Dutchess County, New York. Proc. Northeast. Weed Control Confer. 15: 539-544.

438. Pierce, M. E. 1961a. Progress report on the effect of Kuron applications after one and two years at Long Pond, Dutchess County, New York. Proc. Northeast. Weed Control Confer. 15: 545.

439. Polteracka, J. 1960. Control of filamentous algae. Gospodarka Rybna, Warsaw 12(4): 16-18.

440. Porter, K. G. 1972. A method for the *in situ* study of zooplankton grazing effects on algal species composition and standing crop. Limnol. & Oceanogr. 17: 913-917.

441. Porter, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature 244(5412): 179, 180.

442. Porter, K. G. 1977. The plant-animal interface in freshwater ecosystems. Amer. Sci. 65: 159-170.

443. Prescott, G. W. 1932. Copper sulphate as an algicide in lakes and reservoirs. Collecting Net 7(8): 196, 197.

444. Prescott, G. W. 1938. Objectionable algae and their control in lakes and reservoirs. Louisiana Municip. Rev. 1(1):

445. Prescott, G. W. 1948. Objectionable algae with reference to the killing of fish and other animals.

446. Prescott, G. W. 1956. Guide to the literature on ecology and life histories of the algae. Bot. Rev. 22(3): 167-240.

447. Price, C. A. and Estrada, M. T. G. 1964. Chlorophyll formation in *Euglena* as a test for herbicides. Weeds 12(3): 234, 235.

448. Provasoli, L., Hutner, S. H. and Packer, L. 1951. Destruction of chloroplasts by streptomycin. Cold Spring Harbor Symposia, Quant. Biol. 16: 113-120.

449. Raab, F. 1931. Taste and odor troubles in the Minneapolis water supply. Jour. American Water Works Assoc. 23(3): 430-434.

450. Raadsveld, W. 1934. Practical applications of oliodynamic action. Chemische Weekblad 31: 505.

451. Rafter, G. W. 1890. Deterioration of water reservoirs, its cause and prevention. Ann. Rep. New Jersey Bd. Health 14: 11, 12.

452. Rai, C. *et al.* 1963. Bensimidazole-metal complex algicides. U.S. Patent 3,101,319.

453. Reed, C. H. 1965. How to treat algae under ice. Water Works & Waste Eng. 2: 12,59.

454. Reich, K., and Aschner, M. 1947. Mass development and control of the phytoflagellate Prymnesium parvum in fish ponds in Palestine. Palestine Jour. Bot. (Jerusalem) 4: 14-23.

455. Reifschneider, W. 1964. a Omega-halopolythiothers. U.S. Patent 3,100,801.

456. Revis, P. R. 1925. Copper sulphate sown on ice of Cheyenne water works reservoir. Eng. News Rec. 94: 660, 661.

457. Ringer, W. C. and Campbell, S. 1955. Use of chlorine dioxide for algae control at Philadelphia. Jour. American Water Works Assoc. 47: 740-

458. Riser, D. 1959. Reducing algae, tastes and odors with copper sulfate and activated carbon. Water Works Eng. 112: 40, 41.

459. Rivers, C. 1964. Virus pesticides. Discovery 25: 27-31.

460. Roberg, M. 1932. Ein Beitrag zur Stoffwechselphysiologie du Grunalgen. II. Ueber die Wirkung von Eisen- und Kupersalzen. Jahrb. f. Wiss. Bot. 76: 311-332.

461. Rodhe, W. 1948. Sjon Norrvikens vattenbeskaffenhet ar 1946-47 och wattenblommingens bekampande med Koppersulfat sommaren 1947. Vattenhygien Fasc, 2: 38-61.

462. Rohm & Haas Company. 1951. Hyamine 2389. Company Bull., Washington Sq., Philadelphia, p. 13.

463. Rollins, F. L. 1936. Discussion of algae problems at Barberton. 15th Ann. Rep. Ohio Confer. Water Purification, Cleveland. 58 pp.

464. Rose, E. T. 1952. Control of blue-green algae at North Twin Lake. Iowa Quart. Biol. Rep. 4(2): 50-57.

465. Rose, E. T. 1954. Blue-green algae control at Storm Lake. Iowa Acad. Sci. Proc. 61: 604-614.

466. Rosenberg, D. G. 1964. Helicopter application of copper sulphate. Taste & Odor Control Jour. 30(8): 2-7.

467. Safferman, R. S. 1968. Virus disease in blue-green algae. In: Algae, Man and Environment. pp. 429-439.

468. Safferman, R. S. and Morris, M. E. 1962. Evaluation of natural products for algicidal properties. Appl. Microbiol. 10: 289-292.

469. Safferman, R. S. and Morris, M. E. 1963. Algal virus; isolation. Science 140 (3567): 679, 680.

470. Safferman, R. S. and Morris, M. E. 1964. Control of algae with viruses. Jour. American Water Works Assoc. 56: 1217-1224.

471. Safferman, R. S. and Morris, M. E. 1964a. Growth characteristics of the blue-green algal virus LPP-1. Jour. Bacteriol. 88: 771-775.

472. Safferman, R. S. and Morris, M. E. 1967. Observations on the occurrence, distribution, and seasons; incidence of blue-green algal viruses. App. Microbiol. 15(5): 1219-1222.

473. Safferman, R. S., Morris, M. E., et al. 1969. Serological and electron microscope characteristics of a new group of blue-green algal viruses (LPP-2). Virology 39: 775-780.

474. Safferman, R. S., Rosen, A. A. et al. 1967. Earthy-smelling substances from a blue-green alga. Environ. Sci. & Tech. 1: 429, 430.

475. Safferman, R. S., Schneider, et al. 1969. Phycovirus SM-1: a virus infecting unicellular blue-green algae. Virology 37: 386-395.

476. Sanders, R. 1944. Chemical methods for the control of algae and scale. Brewers Digest 19: 53-55.

477. Sarig, S. and Lahav, M. 1961. New substances for control of Prymnesium. Lignasan Bamidgeh 13: 3-8.

478. Sampiero, G. 1925. La destruction des algues des rizieres par le sulphate de cuivre. Giornale di Risicoltura 1925:

479. Sawyer, C. N., Lackey, J. B. and Lenz, A. T. 1944. Investigation of the odor nuisance occurring in the Madison lakes particularly Monona, Waubesa, Kegonsa from July 1943 to July 1944. Madison, Wisconsin. Mimeogr.

480. Saxena, P. N., Amala, D. V. and Ahmad, M. R. 1979. Algistatic and and algicidal effects of Panicide. Indiana Jour. Exper. Biol. 17(2): 223, 224.

481. Schneider, I. R., Diener, T. O. and Safferman, R. S. 1964. Blue-green algal virus LPP-1: purification and partial characterization. Science 144: 1127-1130.

482. Schoenfeld, C. 1957. Don't let 'em spray. Field & Stream 52(4): 46, 79-81.

483. Schoenfeld, C. 1950. The case against copper. Hunting & Fishing 1950: 11, 12.

484. Scott, R. M. 1952. Algal toxins. Public Works 83: 54, 55.

485. Senior, V. E. 1960. Algal poisoning in Saskatchewan. Canadian Jour. Comp. Med. & Vet. Sci. 21(1): 26. (24: 26 ?).

486. Service, W. S. 1963. How to fight algae. Aquarium Jour. 34(1): 387-388.

487. Seshadri, K. and Buch, S. D. 1958. Elimination of algae in Sambhar Lake by chlorination. Jour. Sci. Indian Res. 17A: 455-457.

488. Seydel, H. 1938. A new method of weed control in lakes and reservoirs. Water & Sewage Works 85(7): 688-

489. Shane, M. S. 1963. How to black out algae. Water Works Eng. 116: 552, 553.

490. Shane, M. S., Cannon, R. E. and DeMichele, E. 1972. Pollution effects on phycovirus and host algae ecology. Jour. Water Pollution Control Fed. 44(12): 2294-2302.

491. Shaner, H. L. 1925. The impounding reservoir, its troubles and remedies. Jour. American Water Works Assoc. 13(5): 531-543.

492. Shapiro, J. 1973. Blue-green algae: why they become dominant. Science 179: 382-384.

493. Shelanski, M. V. 1954. Delrad Hercules experimental algicide. Tech. Serv. Bull., Hercules Powder Co. No. 203.

494. Shelubsky, M. 1951. Toxic blue-green algae in fish ponds in Israel. Bamidgeh Bull. Fish Cult. in Israel 3: 49, 50; 146-154.

495. Shelubsky, M. 1952. The use of copper sulphate as a control measure against objectionable algae blooms in fish-ponds. Bamidgeh Bull. Fish. Cult. in Israel 4: 3, 4, 59.

496. Sherwood, R. C. 1955. Effective algae control. Beach & Pool 29: 25.

497. Shilo, M. 1951. Observations on the properties of a toxin produced by *Microcystis*. Verh. Intern. Ver. Limnol. 11: 362-366.

498. Shilo, M. 1953. Conditions which determine the efficiency of ammonium sulphate in the control of *Prymnesium parvum* in fish breeding ponds. Appl. Microbiol. 1: 330-333.

499. Shilo, M. 1965. Study on the isolation and control of blue-green algae from fish ponds, Bull. Fish Cultur. Israel 17: 83-93.

500. Shilo, M. 1967. Formation and mode of action of algal toxins. Bacter. Rev. 31: 180-193.

501. Shilo, M. 1968. New approaches in the control of economically important harmful brackish and fresh water algae. Confer. on Global Impact of Appl. Microbiol. Addis Ababa. (In Press, 1967).

502. Shilo, M. 1970. Lysis of blue-green algae by a Myxobacter. Jour. Bacter. 104: 453-461.

503. Shilo, M. 1971. Biological agents which cause lysis of blue-green algae. Mitt. Intern. Ver. Limnol. 19: 206-213.

504. Shilo, M. and Shilo, M. 1954. Control of the phytoflagellate *Prymnesium parvum*. Verh. Intern. Ver. Limnol. 2:

505. Shimanskii, B. A. 1963. Active measures in controlling overgrowth in cooler-reservoirs. Trudy Vses Gidrobiol. Obshch. 14: 74-114. (Russ.)

506. Siems, V. B. 1930. Overcoming algae troubles in a clear water reservoir. Water Works Eng. 83: 739, 740.

507. Sigrowth, E. A. 1957. Control of odor and taste in water supplies. Jour. American Water Works Assoc. 49: 1507-

508. Sikka, H. C. and Pramer, D. 1968. Physiological effects of fluometron on some unicellular algae. Weed Sci. 16: 296-299.

509. Simons, R. E. 1951. Combating tastes and odors due to algae. Taste & Odor Control Jour. 17(3): 2-

510. Singh, R. N. and Singh, P. K. 1967. Isolation of cyanophages from India. Nature 216: 1020, 1021.

511. Sladeckova, A. 1969. Control of slime and algae in cooling systems. Verh. Intern. Ver. Limnol. 17: 532-536.

512. Sladeckova, A. and Sladeck, V. 1968. Algicides- friends or foes? In: Algae, Man and Environment. pp. 441-458.

513. Smith, G. M. 1924. Ecology of the plankton algae in the Palisades Interstate Park, including the relation of control methods to fish culture. Roosevelt Wild Life Bull. 2(2): 91-195.

514. Smith, K. N. and Brown, R. M. 1967. Ultrastructure and time-lapse studies on the replication cycle of the blue-green algal virus LPP-1. Virology 31: 329-337.

515. Smith, K. M., Brown, R. M., Walne, P. L. and Goldstein, S. A. 1966. Electron microscopy of the infection process of the blue-green algal virus. Virology 30: 182-192.

516. Smith, K. M., Brown, R. M., Goldstein, D. A. and Walne, P. L. 1966. Culture methods for the blue-green alga Plectonema boryanum and its virus with an electron microscope study of virus-infected cells. Virology 28: 580-591.

517. Smith, M. W. 1935. The use of copper sulphate for eradicating the predatory fish population of a lake. Trans. American Fish. Soc. 65: 101-114.

518. Smith, P. 1934. Methods of applying copper sulphate at Baltimore, Maryland. Water & Sewage Works 81: 135, 136.

519. Snow, E. A. and Iantosca, A. 1952. Treating algae under ice at Westfield, Mass. Jour. New England Water Works Assoc. 66: 47-54.

520. Snow, J. R. 1956. Algae control in warmwater hatchery ponds. Proc. 10th Ann. Confer. Southeast Assoc. Game & Fish. Comm. 1965: 80-85.

521. Snow, J. R. 1963. Simazine as an algicide for bass ponds. Progr. Fish Cultur. 25(1): 34-36.

522. Snow, W. B., *et al*. 1957. Control of aquatic plants and algae in potable water and watersheds. Panel Disc. Northeastern Weed Control Proc. (In Press, 1957).

523. S-(1,2-Dichlorovinyl) cysteine. U.S. Patent 2,890,246. 1959.

524. Sopp, C. W. 1936. Plankton control in Norris Reservoir. Jour. American Water Works Assoc. 28(4): 447-457.

525. Sopp, C. W. 1936a. How plankton are controlled at Pasadena. Water Works Eng. 89: 189-192.

526. Spannuth, D. 1929. New methods for preventing alga formation in public baths. Gesundh.-Ing. 52: 329-

527. Stanker, L. H. and Hoffman, L. R. 1979. A simple histological assay to detect virus-like particles on the green alga *Cylindrocapsa* (Chlorophyta). Canadian Jour. Bot. 57(7): 838-842.

528. Stepanek, M. and Chalupa, J. 1959. Algicide CA-350 in practice. Vidni hospod. 6: 281-283. (Czech.)

529. Stepanek, M., et al. 1960. Application of the algicide CA-350 in reservoirs. Sborn. Vysoke Skoly Chem.-Tech. Praze, Fak. Tech. Paliv a Vody 4(2): 375-402.

530. Stepanek, M., Vlcek, V. and Cervenka, R. 1962. Algicide effects of some antibiotics. Sci. Pap. Inst. Chem. Technol. Prague 5: 333-346.

531. Stewart, E. P. 1941. Copper sulphate applied as a spray for algal control. Water Works Eng. 94(12): 617-

532. Stewart, J. R. and Brown, R. M. 1969. Cytophaga that kills or lyses algae. Science 164: 1523, 1524.

533. Strauss, J. 1963. Water treatment facilities lick algae problems. Public Works 94(4): 94, 95.

534. Strauss, J. 1963a. Pre-treatment licks algae problems. Water & Sewage Works 110(7): 267-268.

535. Strauss, M. W. 1949. Control of weeds in irrigation systems. U.S. Dept. Interior, Bur. reclamation. pp. 1-140.

536. Sundholm, N. K. and Hubbard, W. L. 1959. Algicides from quinone derivatives. U.S. Patent 2,999,810.

537. Surber, E. W. 1950. Control of aquatic growths in impounding reservoirs. Jour. American Water Works Assoc. 42: 735-740.

538. Surber, E. W. 1950a. The relative value of 2, 4-D sodium arsenite and copper sulphate in controlling pond scum algae. Proc. 7th Ann. Meet. North Central Weed Control Confer. 1950: 108-110.

539. Svec, J. and Benesova, J., et al. 1961. Report on the results of a treatment with algicide of the Frystak Reservoir. (Czech.). Cesk. Hyg. 6(1): 55, 56.

540. Swartz, S. C. 1950. Algae control and method of enumeration. Jour. New England Water Works Assoc. 64(1): 72-76.

541. Sweeney, O. R. 1941. Methods of maintaining the proper copper concentration in the treatment of water. Proc. Iowa Acad. Sci. 48: 259-

542. Swift, D. C. 1956. Four water-treatment methods to remove algae, hardness, and dissolved solids. Power 100(5): 88, 89.

543. Swingle, H. S. 1968. Fish kills caused by phytoplankton blooms and their prevention. Fed. A O Fish. Rep. 44(5): 407-411.

544. Swingle, W. T. 1896. Bordeaux mixture: its chemistry, physical properties, and toxic effects on fungi and algae. U.S. Dept. Agric. Div. Veg. Physiol. & Path., Bull. 9. 37 pp.

545. Swinyard, T. C. 1962. Compositions containing 2,4,5,-trichlorophenol for the prevention of fungi and algal growths. U.S. Patent 3,034,953.

546. Symon, K., Cervenska, R., et al. 1960. K Problemu Vodmich Kvetu V Hygien Vody. I. Slgicidal preparat CA-350 a toxicita vornich kvetu. Ceskoslovenska Hyg. 5(8): 485-490.

547. Taft, C. E. 1945. The algologist and water sanitation. Ohio Jour. Sci. 45(3): 97-102.

548. Taft, C. E. 1949. The algologist's part in city and industrial water supply problems. Limnol. Aspects of Water Supply and Waste Dispersal. Amer. Assoc. Adv. Sci. 1949: 74-78.

549. Taft, C. E. 1949a. How to combat algae in industrial water supplies. Plant Eng. 3(6): 37, 38.

550. Tarlton, E. A. 1948. Algae control at Danbury, Connecticut. Jour. New England Water Works Assoc. 63: 165-

551. Tarlton, E. A. 1949. Algae control, experiences and practices at Danbury, Conn. Water & Sewage Works 96(6): 221-224.

552. Tate, H. D. and O'Brien, G. E. 1961. Dichlone as a control for algae and submersed aquatics. Proc. 13th North Central Weed Control Conference.

553. Tatton, J. O. G. and Ruzicka, J. H. A. 1967. Organochlorine pesticides in Antarctica. Nature 215: 346.

554. Tauson, A. O. 1934. Effect of chlorination on water organisms. Bull. Inst. Rech. Biol. Univ. Perm 9: 251-263.

555. Taylor, E. W. 1955. The control of algal growths in a small reservoir by intermittent chlorination. Proc. Intern. Assoc. Theor. & Appl. Limnol. 12: 671-674.

556. Taylor, G. R. 1925. Winter treatment of algal growths. Eng. Contract. 63: 123, 124.

557. Thomas, D. O. 1916. Outriggers and pulleys facilitate $CuSO_4$ treatment. Eng. Rec. 74: 644.

558. Thomas, N. A. 1940. Taste and Odor control on Lake Michigan. Jour. American Water Works Assoc. 32(7): 1183-1186.

559. Thornton, M. K. and Ulich, W. L. 1955. Removing green scum (algae) from tanks and reservoirs with bluestone. Texas Agric. Exten. Serv. L-55. 1 p.

560. Tiffany, R. K. 1918. Control of algae in irrigation canals by $CuSO_4$. U.S. Reclamation Rec. 1918. (Eng. Contract. 50: 558).

561. Tisdale, E. S. 1936. Water pollution control in West Virginia. Proc. 10th Amer. Conf. on Water Purification. West Virginia Univ. Tech. Bull. 8: 126-132.

562. Tommons, F. L. 1954. Control of algae with rosin amine D acetate. U.S. Dept. Agric., Weeds

563. Tobiska, J. W. 1949. Algae nuisance in water supply. Colorado A&M News, June, 1949. 1 p.

564. Torres, A. M. R. and O'Flaherty, L. M. 1976. Influence of pesticides on *Chlorella*, *Chlorococcus*, *Stigeoclonium* (Chlorophyceae), *Tribonema*, *Vaucheria* (Xanthophyceae) and *Oscillatoria* (Cyanophyceae). *Phycologia* 15(1): 25-36.

565. Toth, R. and Wilce, R. T. 1972. Virus-like particles in the marine alga *Chorda tomentosa* Lyngbye (Phaeophyceae). Jour. Phycol. 8: 126-130. 6 figs.

566. Tressler, W. L. 1937. The effects of $CuSO_4$ treatment on certain genera of freshwater plankton organisms. Intern. Rev. Ges. Hydrobiol. Hydrograph. 35: 178-186.

567. Tressler, W. L. and Bere, R. 1938. A limnological study of Chatauqua Lake. New York Conserv. Dept. Biol. Surv. 12: 196-213.

568. Ueda, K. 1966. Virus-like structures in the cells of the blue-green alga *Oscillatoria princeps*. Exper. Cell. Res. 40: 671-673.

569. Unexcelled Chem. Corp. 1947. A report on algal control in fish hatchery tanks. New York.

570. United States Rubber Co. 1954. Control of bloom-producing blue-green algae. Bethany Information Sheet No. 75. 2 pp.

571. United States Rubber Co. Information Sheet No. 82A.

572. United States Rubber Co. 1961. Herbicides and algicides, Brit. Patent 862,857.

573. Vaczi, L. 1943. Effects of redox dyestuffs on the longevity of plankton in Lake Balaton. Arb. Ungarisch. Biol. Forsch. 15: 528-532.

574. Van Arnum, W. I. 1938. Method of treating lakes and reservoirs with copper sulphate for the control of algae. Ohio State Agric. Div. Conserv., Bull. 20-5. Mimeographed.

575. Vanvuuren, L. R. J. and Vanvuuren, F. A. 1965. Removal of algae from waste-water maturation pond effluent. Jour. Water Pollut. Control Fed. 37: 1256-1262.

576. Vaughn, J. C. 1972. Special lake water treatment problems. Jour. American Water Works Assoc. 64: 585-589.

577. Venkataraman, G. S., Kaushik, B. D., et al. 1973. Cyanophage AC-1: a phage infesting unicellular and colonial blue-green algae. Current Sci. 42(3): 104, 105.

578. Vrhovsek, D. 1975. The effect of different light intensity, temperature, pH and concentrations of pesticide Orga-T on algal composition. Biol. Vestn. 23(1): 75-88.

579. Wacker, J. E. and Martin, E. L. 1977. The characterization of a possible biological control agent SM-2 for blue-green algal blooms. Proc. Nebraska Acad. Sci. Affil. Soc. 87: 77-

580. Waldeck, K. 1941. Local problems and remedies. Water Works Eng. 94(5): 244.

581. Wallace, T. C. 1949. Control of cooling tower algae with chlorine gas. Gas 15(9): 37.

582. Walsby, A. E. 1970. The nuisance algae: curiosities in the biology of planktonic blue-green algae. Jour. Soc. Water Treat. & Exam. 19(4): 359-373.

583. Waring, F. H. 1922. Methods of overcoming algae trouble in the operation of water purification plants using river water as a source of supply. Ohio Dept. Health Confer. Water Purification IInd Ann. Rep.

584. Warrick, L. F. and Muegge, O. J. 1932. Taste and odor removal. Jour. American Water Works Assoc. 24(2): 242-248.

585. Warrick, L. F., Wirth, H. E. and Van Horn, W. 1943. Control of microorganisms and aquatic vegetation. Water & Sewage Works 90(7): 267-272.

586. Weber, H. 1933. Vergiftungsversuche mit Kupersulfat. Zeit. f. Hydrol. 1933: 64-104.

587. Weers, E. T. and Zaret, T. M. 1975. Grazing effects on nannoplankton in Gatun Lake, Panama. Verh. Intern. Ver. Limnol. 19: 1480-1483.

588. Wehner, D. C. 1964. Controlling algae with alkyl guanidine salts. U.S. Patent 3,142,6515.

589. Weir, P. 1948. Copper sulphate--Some aspects of its usefulness and methods of application. Water & Sewage Works 95 (Ref. & Data Sec.): R152-R154.

590. Welch, W. A. 1963. Potassium permanganate in water treatment. Jour. American Water Works Assoc. 55: 735-

591. Whipple, G. C. 1927. The Microscopy of Drinking Water. John Wiley & Sons, New York.

592. Whipple, G. C., Fair, G. M. and Whipple, M. C. 1948. The Microscopy of Drinking Water. John Wiley & Sons, New York.

593. Whitshead, R. C. 1948. Shustoke Reservoir: Biology and algal control. Jour. Inst. Water Eng. 2: 577-

594. Willcomb, G. E. 1935. *Synura* troubles at Albany, New York. Jour. American Water Works Assoc. 27(6): 742-748.

595. Williams, A. E. 1953. Control of slime and algae in cooling water systems. Cheap Steam 37: 74, 75.

596. Williams, O. B., Groninger, C. R. and Albritton, N. F. 1952. The algicidal effects of certain quaternary ammonium compounds. Prod. Monthly 16(8): 14, 15.

597. Wilson, C. 1931. Chlorine control of certain algae growths in Los Angeles reservoirs. Western City 7(10): 25.

598. Wirster, C. F. 1968. DDT reduces photosynthesis by marine phytoplankton. Science 159: 1474, 1475.

599. Wisenbaker, R. E. 1942. Control of algae in reservoirs. Proc. 24th Ann. Texas Water & Sewage Works, Short School.

600. Woodhull, R. S. 1955. Tastes and odors in Connecticut water supplies. Jour. New England Water Works Assoc. 69(2): 126-139.

601. Wright, S. J., Stainthorpe, F. and Downs, J. D. 1977. Interactions of the herbicide propanil and a metabolite 3,4-dichloroaniline with blue-green algae. Acta Phytopath. Acad. Sci. Hungary 12(1/2): 51-60.

602. Wu, J. H., Choules, G. L. and Lewin, R. A. 1968. Early stages of the infection process in a blue-green algal virus system, as affected by KCN and light. In: Biochemical Regulation in Diseased Plants or Injury, Phytopath. Soc. Japan. pp. 153-160. 1968.

603. Wu, J. H. and Lewin, R. A. 1967. Photoreactivation of UV-irradiated blue-green algal virus LPP-1. Virology 31: 657-664.

604. Wu, J. H., Lewin, R. A. and Werbin, H. 1967. Photoreactivation of UV-irradiated blue-green algal virus LPP-1. Virology 31: 657-664.

605. Wu, J. H. and Shugarman, P. M. 1967. Effect of virus infection on rate of photosynthesis and respiration of a blue-green alga, *Plectonema boryanum*. Virology 32: 166, 167.

606. Wurtsbaugh, W. A. and Apperson, C. S. 1978. Effects of mosquito control insecticides on nitrogen fixation and growth of blue-green algae in natural plankton associations. Bull. Environ. Contam. Toxicol. 1978: 641-647.

607. Yashouv, A. 1955. Filamentous algae in fish ponds. Bamidgeh, Bull. Fish Culture in Israel 7(1): 10-12.

608. Yvon, A. 1956. Action of a-naphthaleneacetic acid on growth of *Chlorella pyrenoidosa*. Compt. Rend. Acad. Sci., Paris 242: 1205-1207.

609. Zavarzina, N. B. 1961. A lytic agent in cultures of *Chlorella pyrenoidosa* Pringsh. Dokl. Akad. Nauk SSSR 137: 291-293. (Biol. Sci. Sec. Transl.).

610. Zavarzina, N. B. 1963. The effect of antibiotics on lysis of culture of *Chlorella pyrenoidosa* Pringsh. Microbiol. 31: 810-812.

611. Zavarzina, N. B. and Protsenko, A. E. 1958. The lysis of *Chlorella pyrenoidosa* Pringsh. cultures. Dokl. Akad. Nauk SSSR 122: 840-843. (Biol. Sci. Sec. Transl.)

612. Zehnder, A. 1951. Uber den Einfluss antibiotischer Stoffe auf des Wachstum von Grunalgen. Experientia 7: 99-

613. Zehnder, A. and Hughes, E. O. 1958. The antialgal activity of actidione. Canadian Jour. Microbiol. 4: 399-408.

WORKSHOP SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

Victor W. Lambou,* William D. Taylor, Jeffrey J. Janik,
Stephen C. Hern, Linda S. Blakey, Marsha K. Morris

Summary

Excessive algal growth in lacustrine waters often requires specialized management and control measures to avoid environmental problems. During March 9-12, 1980, a workshop was held at the Asilomar Conference Center, Pacific Grove, California, for the following purposes:

- a. To review state-of-the-art techniques for the management and control of lacustrine algal populations.
- b. To establish the functional availability and limits of various algal management and control techniques.
- c. To determine research needs in relations to the further development of algal management and control techniques.

Twenty-seven individuals participated in the Workshop. Invited speakers were chosen so as to provide an interdisciplinary approach to discussions of algal management and control.

Victor Lambou, in opening the Workshop, posed the following questions to the participants:

- a. How accurately can algal populations resulting from specific algal management and control techniques be predicted?
- b. What conditions are necessary for specific algal management and control techniques to be successful?
- c. Can lacustrine waters be classified by the type of algal management and control technique likely to succeed?
- d. Are there specific algal management and control techniques for individual species or groups of species of problem algae?
- e. When is it feasible to apply algal management and control techniques to an entire water body?

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* Lambou and Hern are of the U. S. Environmental Protection Agency, Las Vegas, Nevada. All others are of the University of Nevada at Las Vegas.

f. When is it feasible to apply algal management and control techniques to localized problem areas in a water body?

g. Under what conditions is it feasible to achieve permanent control of problem algae?

h. What algal management and control techniques have been adequately developed and tested?

i. What algal management and control techniques need further development and testing?

j. How close to development, in terms of time and resources, are promising new algal management and control techniques?

Until very recently algal management and control efforts consisted almost entirely of using toxicants to treat the symptoms rather than the cause of the problem. Furthermore, only recently has any appreciable amount of research been conducted in a systematic fashion toward the development of innovative algal management and control techniques. The Workshop participants emphasized that research on biological control and control by nutrient reduction techniques is in its infancy. Knauer, pointed out that algal management and control techniques, besides those involving toxicants, have been used successfully by state agencies; however, the techniques are expensive and the results are often unpredictable. Knauer further pointed out that much of the public believes that the lake manager has a large "bag of tricks" which can be used to cure almost any algal problem. There is no bag of tricks and presently no practical permanent solution to algal problems.

As Wetzel pointed out, all lacustrine waters go through a successional pattern of fertility and primary productivity. The species composition and abundance of the phytoplankton, periphyton, and macrophyte communities as well as their relative importance follow fairly predictable patterns over time. Considering this, algal problems are inevitable in most bodies of water. Because of the existence of this successional pattern, there are bounds or limits outside of which it is impossible to prevent or control algal problems without applying massive therapeutic treatments. Wetzel stressed the need for a much better understanding of the causes of algal problems so that lake managers will know when it is feasible to apply environmental and ecological algal management and control techniques and when it is not feasible to prevent or control algal problems. Even within the same geographic region, variability in morphometry and dissolved and particulate constituents result in differences in algal populations. These variables must be taken into consideration in developing and applying algal management and control techniques.

The discussions brought out the importance of knowing why an "algal problem" is a problem, i.e., what beneficial use of water is being adversely impacted? Are algae impacting aesthetics, fishing, recreation, swimming, potable water, wildlife, etc.? Given our present state of knowledge, it is often difficult to predict what effect changing the species composition and abundance of an algal community will have on water uses. Reducing the size of an algal population to benefit aesthetics may adversely impact a fishery. The decision as to what beneficial use an algal population should be managed for, or how conflicts between competing goals should be compromised, are not ecological or limnological questions. However, limnologists and ecologists are responsible for predicting the impact of specific algal management and control techniques on water uses.

Prescott, in his review of algal control measures, stated that the toxicant copper sulfate has proved to be safe and reliable for reducing algal populations. In fact, he concluded that it has been and still is the most widely used method of algal control since its first application in the late 1880's. According to Fitzgerald, the increasing cost of copper sulfate has led to more efficient use of copper through the continuing development of chelators and synergistic chemicals.

Oswald emphasized that there are no economically reliable mechanical methods to manage or control algal populations. Currently used methods are centrifugation and filtration. Shapiro mentioned that low energy propeller devices have been successfully used to move problem surface algal scums away from localized nearshore areas. There was a consensus that if reliable mechanical methods could be developed, they would be appropriate mainly for localized high-use areas such as beaches.

Removing nutrients before they enter lacustrine waters is an approach to algal management and control which addresses one of the basic causes of algal problems. Techniques for the control of nutrient-rich source waters include diverting water flows around a water body, processing of source water by a wastewater treatment plant, and applying source waters to land areas through spray irrigation. However, these techniques are quite expensive. Larsen identified several very important aspects of nutrient source control which need to be examined more closely. Further study of the factors controlling the availability of phosphorus to algae is necessary. Larsen also pointed out that our knowledge of the importance of storm events as sources of nutrients to water bodies is very deficient. He also identified the effects of different land-use practices on export of nutrients to water bodies as needing further study.

Once nutrients are abundant enough to support a problem algal population in a water body, there are methods to reduce their abundance or make them less available to algae. The use of dilution/flushing of nutrients, chemical inactivation and precipitation of nutrients, aeration, and altered discharge depth as algal management and control techniques were discussed.

The applicability of dilution/flushing to algal management and control was discussed by Welch. This technique can be used to reduce the level of nutrients in large or small water bodies. Successful results are dependent upon the quantity and quality of the dilution water. The technique is definitely successful if low nutrient content dilution water is available; however, it also may be successful if dilution water of moderate nutrient content is available. Welch stated that in the water bodies he studied flushing led to a reduction in blue-greens and a shift towards diatoms. The shift in algal community structure may have been due to the dilution of blue-green excretory products. Welch found that algal populations can be reduced by relatively low rates of water exchange on the order of 0.5-1.0%/day of continuous input or interspersed periods of high flow during the spring-summer growth period. Algal populations can be kept at a satisfactory level if sufficient dilution/flushing water is available.

Both Cooke and Knauer stated that treatment of water bodies with alum is effective in inactivating and precipitating phosphorus, making it unavailable for the production of algae. Alum is particularly useful for inactivating phosphorus when maximum soluble reactive phosphorus concentrations are present. The water body must be stratified to prevent perturbations to the flocculent layer by wind mixing. Since pH values less the 6 result in toxic concentrations of Al^{+++}, water bodies with low alkalinity (30-40 mg $CaCO_3$/l) are susceptible to pH shifts and should not be treated with alum. It was suggested that less toxic compounds such as zirconium be developed as flocculents. Alum treatment may enhance macrophyte growth due to increased water transparency. Cost and logistics restrict alum treatments to small water bodies with residence times of 8 months to 1 year or more.

Methods of applying alum are inefficient and need to be improved. Data on the cost-benefit of treating water bodies with alum are not available due to the absence of adequate long-term evaluation of treatment effectiveness. Also, additional data on the doses of alum required to meet algal management and control objectives are needed.

The management and control of algal populations through artificial aeration/circulation was reviewed by Lorenzen. He stressed that inconsistencies in results obtained from applying this technique are possibly due to wide variations in the application procedures used. Artificial aeration/circulation is an effective method for destratifying water bodies or preventing stratification from occurring and thereby controlling algal populations and species composition even when nutrient concentrations are relatively high. Lorenzen recommended that 9.2 m^3/min of air per $10^6 m^2$ of water body surface be applied to the deepest portion of the water body before thermal stratification in the spring to prevent stratification. The lack of stratification increases the mixed depth of algae and can reduce algal production due to light limitation. The application of this technique has led to shifts of populations dominated by blue-green algae to populations dominated by the more desirable algae. These shifts may be partially explained by lower pH values after destratification due to increased concentrations of CO_2. Artificial aeration/circulation may cause some problems, e.g., it may eliminate the coldwater habitat at midwater or near the bottom leading to the disappearance of coldwater fishes such as salmonids.

It is possible to lower the thermocline by discharging water from the bottom of the water body. As with artificial aeration/circulation, this will increase the mixed depth of algae and if sufficient it may reduce algae populations due to light limitation. Bottom discharges will also remove nutrient-rich hypolimnetic waters from the system. Although this technique may decrease algal populations in the water body, the discharge water may increase algal populations downstream.

The use of biological algal management and control techniques has largely been ignored. Shapiro pointed out that biological processes have been observed in nature to change algal community species composition and abundance. If we could learn when, where, and how these processes work, they could be used to manage or control algal populations. Biological relationships are slippery, and at our present state of knowledge, it is not possible to predict the effectiveness of biological techniques with any degree of certainty. However, because of biological feedback mechanisms, biological techniques have the potential for being relatively inexpensive and possibly self-perpetuating.

Shapiro stated that high grazer zooplankton populations can effectively control algal abundance and prevent nuisance algal blooms. To emphasize the effectiveness of grazing by zooplankton, Porter pointed out that, in eutrophic water bodies during periods of high zooplankton abundance, the grazers can filter the entire volume of water present as many as 4.7 times during a day. However, according to Wetzel, algal nongrazer losses due to death and sinking exceed grazing losses on the average by a factor of 9 to 1.

Zooplanton grazer populations are often so reduced in numbers by planktivorous fish as to be ineffective in controlling algal populations. Shapiro suggested methods to reduce zooplankton grazer losses through the manipulation of fish-zooplankton-algae interrelationships. An example of this pointed out by him was when muskies were introduced into a small lake, they reduced the number of planktivorous fish, allowing the herbivorous zooplankton population to increase and the zooplankton in turn significantly reduced the population of algae. Winter-kill and the artificial removal of fish populations have been observed to have similar results. The loss of zooplankton grazers to planktivorous fish may be minimized by creating zooplankton refuges in water bodies. Shapiro suggested a refuge for zooplankton could be created by maintaining a narrow bank of highly oxygenated water near the surface of the water body. He felt that this bank of water may be unsuitable for predator fish species due to the high temperature. Shapiro also suggested that an increase in the size (depth) of the epilimnion through artificial aeration would decrease predation intensity on zooplankton.

It was suggested that an external source of food for zooplankton in the form of particulate organic carbon could be utilized to increase zooplankton populations or maintain populations during periods of low algal abundance. Possible sources of particulate organic carbon include diversion of water with high levels of carbon to the water body or stocking it with material rich in particulate organic matter such as hay. Periodic inundation of vegetation by fluctuating water levels would be another approach to increasing particulate organic carbon.

Porter stressed the need to determine the quality of available food and its effect on zooplankton production. She stated that not all species of algae are available to grazers, with algae being grazed in relation to the body size of the grazer. Even the largest zooplankton are unable to graze on large filamentous green and blue-green algae. Zooplankton grazing cannot eliminate the large blue-green algal forms once they are established. An algal management strategy suggested by Shapiro was to use an alternate means to reduce algal populations to a size structure and composition utilized more efficiently by grazers. Crisman found that the large zooplankton common in more northern water bodies were replaced in Florida's subtropical waters by smaller zooplankton species. Florida zooplankton, because of their smaller size are not able to graze on the large algae eaten by their more northern counterparts. In Florida lakes, phytophagous fish take the place of the northern macrozooplankton in the community.

Wetzel felt that biomanipulation of algal populations through the use of pathogens offered the most promise for the effective control of immediate algal problems. Pathogens offer the possibility of a self-perpetuating algal management technique at low cost, making this a very desirable area for further research and development.

Desjardins pointed out that cyanophages meet a number of criteria that support their usefulness in algal management and control. They appear to be specific for the nuisance algal species, are nontoxic to other organisms, and have no direct adverse effect on water quality. Furthermore, they appear to be best suited for prevention rather than elimination of algal problems. To date research on the use of cyanophages has been limited to laboratory and small-scale pond experiments. Survival of cyanophages in the natural environment and the development of resistant hosts are problems that must be critically examined. A thorough program of field testing is urgently needed.

Burnham discussed microbial control of problem algae. This technique appears promising, although research on its use is in its infancy. Laboratory experiments indicate that the genus Myxococcus is especially well suited for the control of problem algae. Myxococcus are more general parasites than they cyanophages, utilizing all cyanobacteria (blue-green algae) for hosts which may give them an advantage over viruses in controlling algae. They possibly could be used to control a range of problem bloom-forming blue-green algal species, while a different virus would be needed to control each problem blue-green species. As in the case of cyanophages, laboratory techniques have not been applied in a field situation.

The use of biological techniques to their full potential requires comprehension of a vast array of complex physical, chemical, and biological relationships. It was suggested that to study these relationships an interdisciplinary team of researchers under the direction of a principal investigator be formed to design and conduct a long-term (at least 3 years) experiment in the application of biological algal management techniques. It was felt that this experiment should be performed on a water body under the complete control of the team. Furthermore, it was felt that the team should be composed of zoologists, biochemists, phycologists, fisheries biologists, microbiologists, chemists, geneticists, and others with unique perspectives which could be directed toward solving algal problems.

A wide variety of approaches to algal management and control were reviewed at this Workshop. The approaches ranged from therapeutic treatments such as algicides and mechanical harvesting, to preventative measures such as nutrient diversion, dilution, and biomanipulation. Most of the methods reviewed, other than the use of toxicants, are relatively new. A recurring area of concern throughout the Workshop was the paucity of adequate evaluations of various algal management and control efforts.

In our opinion, the Workshop was extremely successful in meeting its objectives, even though it was not possible for the participants to give specific answers to all the questions posed to them. Our present state of knowledge does not allow for this. However, the participants most admirably defined where the gaps in our knowledge exist and where research efforts should be emphasized.

The Workshop participants were directed to arrive at conclusions relative to the state-of-the-art of algal management and control techniques and to recommend needed research. These conclusions and recommendations follow.

Conclusions

The following are conclusions of the Workshop participants:

- a. The causes of algal problems are not fully understood. However, it is known that most lacustrine systems undergo a natural succession promoting the eventual inevitability of algal problems. Better methods for managing and controlling algal populations are needed, especially those which remove causes of the problem.
- b. In order to properly design algal management and control programs, it is necessary to know why an algal problem is a problem, i.e., what beneficial use of water and its associated water quality requirements are being interfered with. Water management objectives aimed at a particular beneficial use (e.g., improving a recreational fishery) may conflict with those required for another use (e.g., the reduction in the abundance of algae for aesthetics).
- c. Systematic and extensive evaluations of the effectiveness of most algal management and control techniques have not been made. Also, the limnological characteristics associated with the maximum effectiveness of most algal management and control techniques are not known.
- d. Algicides provide an effective cosmetic treatment of algal problems. Copper is still the agent of choice; however, because of the considerations of cost and toxicity, copper sulfate is being replaced by chelated and synergistic formulations of copper for control purposes.
- e. Many algal management and control techniques, other than those involving the use of toxicants, have been utilized successfully by state agencies; however, their application is expensive and the results from their application are often unpredictable.
- f. The direct removal of algae by mechanical means is presently not economical for managing and controlling algal problems in large bodies

of water. However, the movement of algal scums from localized nearshore areas through the use of artificially induced surface currents may provide a low cost treatment method.

g. Source control of nutrients is an algal management and control technique which addresses the cause of the problem. However, cost-effective source control techniques for nonpoint sources of nutrients are not readily available. Furthermore, it is presently not possible to accurately calculate nutrient export coefficients for various land uses. Information is needed relative to the source of variations in nutrient export coefficients.

h. The effects of reducing the nutrient supply on algal community structure is not fully understood. Techniques for determining the quantity of nutrients which are biologically available to algae are inadequate. The reduction of the level of nutrients in lacustrine waters through dilution/flushing with water of low or moderate nutrient content may result in a reduction of blue-green algae and shift of the community composition in favor of diatoms.

i. Artificial aeration/circulation of lacustrine waters may reduce algal biomass and cause shifts of populations dominated by blue-green algae to populations dominated by the more desirable green algae. However, the results of applying this algal management and control technique have not been consistent. In some instances, artificial aeration/circulation may only partially destratify a water body and can aggravate algal problems due to the release of nutrients from the hypolimnion. The manipulation of thermocline levels may be used as a management and control technique; however, this technique has not been fully developed and tested.

j. Treatment of lacustrine water bodies with alum can precipitate phosphorus in the water column and inhibit the release of phosphorus from bottom sediments. However, very little is known relative to its toxicity, dosage requirements, effectiveness as an algal management and control technique, and efficient application to water bodies. Since pH values of less than 6 result in toxic concentration of aluminum, water bodies with low alkalinity (30-40 mg $CaCO_3$/l) are susceptible to pH shifts and should not be treated with alum. Less toxic compounds, such as zirconium, should be developed as flocculents.

k. Biological processes that change algal community species composition and abundance have been observed to occur naturally, but have rarely been deliberately induced by man to control the abundance and composition of algal populations. Biological methods have the potential for providing low-cost, self-sustaining means to manage and control algal abundance and community composition. The adverse consequences of the improper utilization of biomanipulation techniques may be reduced through biological feedback processes which provide an inherent stability to biological systems. Biomanipulation as an algal management and control technique could be developed most effectively by a team of multidisciplinary experts working on a body of water under their complete control.

l. Biomanipulation of algal populations through the use of viral or bacterial pathogens holds promise as an effective algal management and control technique. To date, these techniques have been limited to laboratory and small-scale pond experiments; practical application of such techniques to natural water bodies appears to be 5-10 years in the future. Cyanophages could provide a species-specific method of preventing (rather than eradication of) blooms of nuisance blue-green algae, but because of host specificity of viral agents, a number of phages would be needed. Very little is known about the factors controlling the survival of cyanophages in natural waters. Myxobacteria (Myxococcus) utilize all cyanobacteria (blue-green algae) for hosts, are not pathogenic to desirable organisms, and have great potential to be developed as a low-cost algal management and control technique.

m. High grazer zooplankton populations can effectively control algal abundance and prevent nuisance blooms. Growth-promoting substances or external sources of food open the possibility to increase the abundance of zooplankton. Because of the complex interrelationships in aquatic biological systems, the results from using grazers as an algal management and control technique is far less precise than the results from using chemical methods.

Recommendations

The following are the recommendations of the Workshop participants:

- a. Systematic and extensive evaluations of the effectiveness of algal management techniques should be made. Also, the limnological characteristics associated with the maximum effectiveness of the various techniques should be determined.
- b. Water quality requirements for specific beneficial uses should be determined so that algae management and control programs can be properly designed to meet them.
- c. The sources of variation in land-use nutrient export coefficients should be determined.
- d. Cost-effective nonpoint source control techniques for nutrients should be developed.
- e. The quantity of nutrients which are biologically available to algae in lacustrine waters should be determined.
- f. The effects of dilution/flushing of nutrients in lacustrine waters on algal community structure and abundance should be more adequately determined. Also, the relationship between the effectiveness of this algal management and control technique and the nutrient content of the dilution/flushing water should be more adequately determined.
- g. Design criteria for the application of aeration/circulation techniques to lacustrine waters for algal management and control should be developed.
- h. The manipulation of thermocline levels in lacustrine waters as an algal management and control technique should be more fully developed and evaluated.
- i. Further work should be conducted on the determination of dosage rates for the use of alum to precipitate phosphorous in the water column and inhibit the release of phosphorous from bottom sediments, the development of more efficient techniques for the application of alum, the determination of the toxicity of alum to aquatic organisms, and the determination of the effectiveness of alum in managing and controlling algal populations.

j. Compounds less toxic than alum, such as zirconium, should be developed as flocculants for use in the management and control of algal populations.

k. The development of chelated and synergistic formulations of copper-based algicides should be continued.

l. Low-energy mechanical devices for movement of surface problem algal scums from localized high-use nearshore areas should be developed.

m. Techniques to biomanipulate algal populations in lacustrine waters should be developed.

n. A team of multidisciplinary experts should develop and evaluate techniques for biomanipulation of algal populations in a body of water under their complete control. This research should be conducted over a long term.

o. Considerable work should be conducted on the development of viral and bacterial pathogens as algal management and control techniques. Work on cyanophages should include the isolation of cyanophages for nuisance algal species, the determination of the effects of lysogeny on algal control and the role of lysogeny in the survival of cyanophages, the determination of the importance of the development of resistant hosts, the determination of the factors controlling the survival of cyanophages in natural systems, and the testing of the effectiveness of presently available cyanophages under field conditions. Work on myxobacteria (Myxococcus) should include the determination of the importance of the development of resistant hosts, the factors controlling their survival in natural systems, and the testing of their effectiveness under natural conditions.

p. A better understanding of the grazing potential of zooplankton populations should be obtained. Work should include the determination of the size spectrum (0.1 μm - 100,000 μm) of particles (bacteria to macroalgae) potentially available to grazers in natural waters, the size of particles various grazers utilize determined by observing the differential removal of particles, and the nutritional value of various particle sizes and types available to grazers.

g. Methods of stimulating the growth of herbivorous zooplankton should be developed.

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